Ministry of Natural Resources

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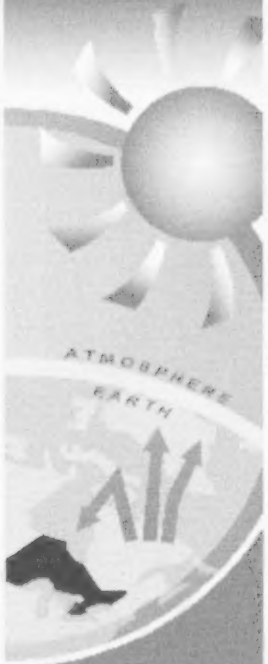
CLIMATE CHANGE RESEARCH REPORT CCRR-36



Responding to Climate Change Through Partnership

Community-Level Effects of Climate Change on Ontario's Terrestrial Biodiversity

Ontario

Sustainability in a Changing Climate: An Overview of MNR's Climate Change Strategy (2011-2014)

Climate change will affect all MNR programs and the natural resources for which it has responsibility. This strategy confirms MNR's commitment to the Ontario government's climate change initiatives such as the Go Green Action Plan on Climate Change and outlines research and management program priorities for the 2011-2014 period.

Theme 1: Understand Climate Change

MNR will gather, manage, and share information and knowledge about how ecosystem composition, structure and function – and the people who live and work in them – will be affected by a changing climate. Strategies:

- Communicate internally and externally to build awareness of the known and potential impacts of climate change and mitigation and adaptation options available to Ontarians.
- Monitor and assess ecosystem and resource conditions to manage for climate change in collaboration with other agencies and organizations.
- Undertake and support research designed to improve understanding of climate change, including improved temperature and precipitation projections, ecosystem vulnerability assessments, and improved models of the carbon budget and ecosystem processes in the managed forest, the settled landscapes of southern Ontario, and the forests and wetlands of the Far North.
- Transfer science and understanding to decision-makers to enhance comprehensive planning and management in a rapidly changing climate.

Theme 2: Mitigate Climate Change

MNR will reduce greenhouse gas emissions in support of Ontario's greenhouse gas emission reduction goals. Strategies:

- Continue to reduce emissions from MNR operations though vehicle fleet renewal, converting to other high fuel efficiency/low-emissions equipment, demonstrating leadership in energy-efficient facility development, promoting green building materials and fostering a green organizational culture.
- Facilitate the development of renewable energy by collaborating with other Ministries to promote the value of Ontario's resources as potential green energy sources, making Crown land available for renewable energy development, and working with proponents to ensure that renewable energy developments are consistent with approval requirements and that other Ministry priorities are considered.
- Provide leadership and support to resource users and industries to reduce carbon emissions and increase carbon storage by undertaking afforestation, protecting natural heritage areas, exploring opportunities for forest carbon management to increase carbon uptake, and promoting the increased use of wood products over energy-intensive, non-renewable alternatives.
- Help resource users and partners participate in a carbon offset market, by working with our partners to ensure that a robust trading system is in place based on rules established in Ontario (and potentially in other jurisdictions), continuing to examine the mitigation potential of forest carbon management in Ontario, and participating in the development of protocols and policies for forest and land-based carbon offset credits.

Theme 3: Help Ontarians Adapt

MNR will provide advice and tools and techniques to help Ontarians adapt to climate change. Strategies include:

- Maintain and enhance emergency management capability to protect life and property during extreme events such as flooding, drought, blowdown and wildfire.
- Use scenarios and vulnerability analyses to develop and employ adaptive solutions to known and emerging issues.
- Encourage and support industries, resource users and communities to adapt, by helping to develop understanding and capabilities of partners to adapt their practices and resource use in a changing climate.
- Evaluate and adjust policies and legislation to respond to climate change challenges.

Community-Level Effects of Climate Change on Ontario's Terrestrial Biodiversity

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Summary

Rapid, anthropogenic climate change has the potential to be a major threat to the biodiversity of terrestrial communities, and is one of the main factors affecting species interactions and ecosystem functioning. Previous reports have described three general mechanisms that can affect species as a result of climate change: demographic, phenological, and genetic, all of which can result in either population expansions or contractions, depending on species-specific responses. In this report, we describe mechanisms that are expected to affect ecological communities, rather than individual species, as a result of climate change.

The effects of climate change on communities and ecosystems are difficult to predict because of complexities and uncertainties associated with biotic interactions. Climate change can significantly affect the genetic composition and structure of communities, and can alter the genetic connectivity among populations, increasing the risk of genetic diversity losses. Climate change typically affects species in communities disproportionately, reducing synchrony and symmetry between interacting species, such as predators and prey. Climate change can also act synergistically with other processes, such as habitat fragmentation, disease, and invasive species, to exacerbate the overall effects. Since individual species responses to climate change vary, some will adapt and remain in a community, others will leave a community, and non-native species may join a community. The result is the potential generation of novel biotic communities, referred to as community reassembly. Community reassembly alters community composition and can therefore lead to changes in biodiversity, species interactions, trophic structure, and ecosystem processes. In this report, we discuss the potential community-level effects of climate change on terrestrial ecosystems, with a focus on wildlife, and identify gaps in knowledge. We also make recommendations for associated management consideration, research needs, and adaptation strategies.

Résumé

Effets au niveau de la communauté du changement climatique sur la biodiversité terrestre de l'Ontario

Un changement climatique anthropique rapide est susceptible de menacer sérieusement la biodiversité des communautés terrestres, et c'est un des principaux facteurs influençant l'interaction des espèces et le fonctionnement des écosystèmes. Des rapports antérieurs ont décrit trois mécanismes généraux qui peuvent avoir une incidence sur les espèces en raison des changements climatiques : les mécanismes démographique, phénologique et génétique, qui peuvent tous entraîner un accroissement ou une diminution de la population, selon les réactions propres aux différentes espèces. Dans le présent rapport, nous décrivons des mécanismes qui devraient influer sur des communautés écologiques, plutôt que sur des espèces données, du fait du changement climatique.

Les effets du changement climatique sur les communautés et les écosystèmes sont difficiles à prédire en raison de la complexité et de l'incertitude des interactions biotiques. Le changement climatique peut avoir une incidence importante sur la composition génétique et la structure des communautés, et peut modifier la connectivité génétique entre les populations, augmentant le risque de perte de la diversité génétique. Le changement climatique influe normalement de façon disproportionnée sur certaines espèces de communautés, réduisant la synchronie et la symétrie entre espèces en interaction telles que les prédateurs et les proies. Le changement climatique peut aussi agir de façon synergique avec d'autres processus, par exemple la fragmentation de l'habitat, la maladie et les espèces envahissantes, pour exacerber les effets globaux. Comme les réactions des diverses espèces au changement climatique varient, certaines s'adapteront et resteront au sein d'une communauté, tandis que d'autres la quitteront et que des espèces non indigènes pourront s'y intégrer. La conséquence est l'apparition potentielle de nouvelles communautés biotiques, ce qu'on appelle le réassemblage de la communauté. La composition de la communauté se trouve ainsi modifiée, ce qui est susceptible d'amener des changements dans la biodiversité, les interactions entre espèces, la structure trophique et les processus écosystémiques. Dans le présent rapport, nous discutons des effets potentiels au niveau de la communauté du changement climatique sur les écosystèmes terrestres, mettant l'accent sur la faune, et nous déterminons les lacunes dans les connaissances. Nous faisons également des recommandations relativement à la gestion, aux besoins en matière de recherche et aux stratégies d'adaptation.

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1.0 Introduction

Climate represents the general weather conditions of a region, including temperature, precipitation, humidity, wind, and other variables, over a long period of time (Garbrecht and Piechota 2006). Climate is affected by interactions between the atmosphere, the ocean, the land surface, the biosphere, and sea ice, as well as latitude, movements of wind belts, topography, and other variables (IPCC 2007). While natural variability in the earth's climate has always existed, over the last century human activities have dramatically increased the rate and degree of climate change (Houghton et al. 2001, IPCC 2007). One of the key causes of current global warming are elevated levels of greenhouse gases, which are the highest they have been for the last 420,000 years (Petit et al. 1999, Houghton et al. 2001).

General circulation models of the earth's climate project that during this century global temperatures may increase by 1.1 to 6.4 °C (IPCC 2007). Mean global surface temperature has already increased by approximately 0.74 °C since the late 1800s (IPCC 2007). Some of the projected changes include global surface temperature increases, precipitation changes (rain, snow, and ice), increased intensity of extreme weather events, sea level rise, reduced snow cover, and reduced sea ice (Galley et al. 2004). Areas at high latitudes, such as Ontario, are projected to be affected more than those at lower latitudes, such as the tropics (IPCC 2007). For example, the projected annual mean temperature increase for Canada's terrestrial ecosystems is 3.1 to 10.6 °C by the 2080s, which is almost double the projected global average temperature change (IPCC 2006). Between 1948 and 2008, average temperatures in Ontario increased by up to 1.4 °C, but changes were more pronounced in the boreal forest and Hudson Bay lowlands regions (Environment Canada 2013). By the end of the century, the average annual temperature in the province is projected to rise by approximately 5 °C (Figure 1; Colombo et al. 2007).

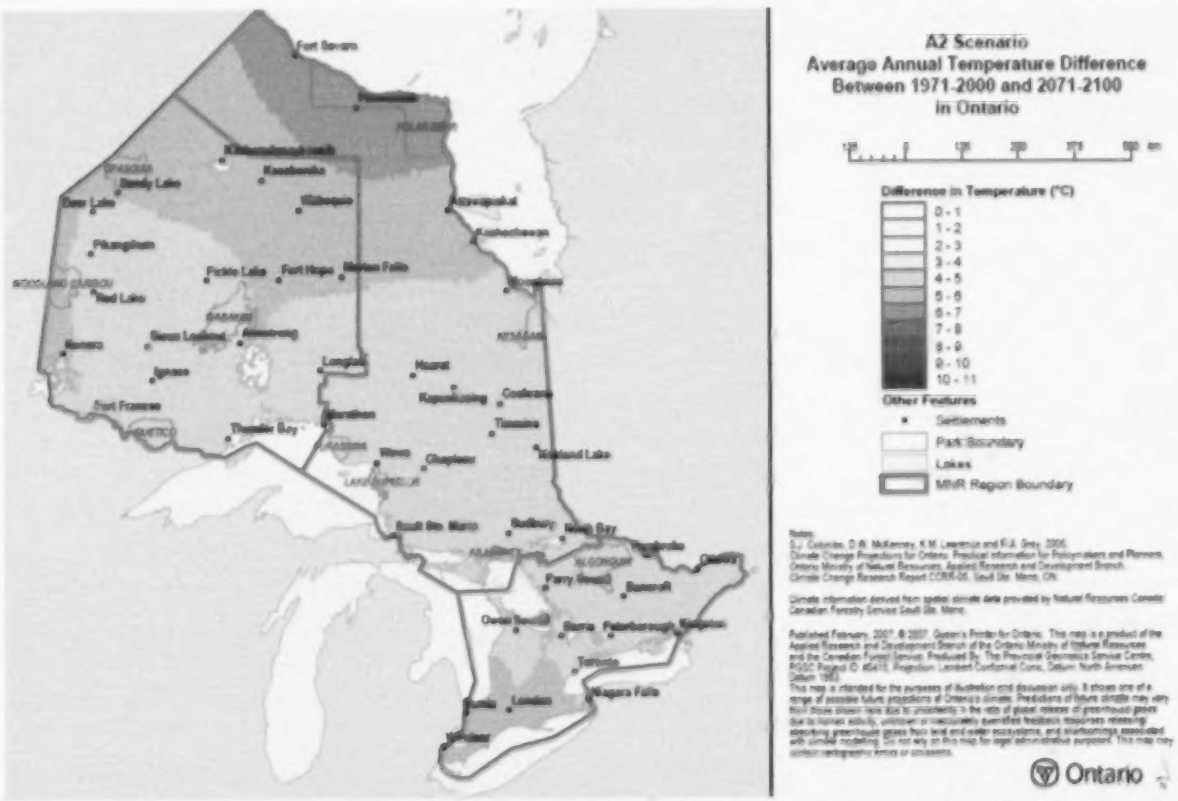

Figure 1. *Projected change in average annual temperature in Ontario for 2071 to 2100 compared to the 1971 – 2000 period, using version 2 of the Canadian Coupled Global Climate Model (CCGCM-A2) (Colombo et al. 2007).*

Climate change is a major threat to biodiversity and an important influence on species interactions and ecosystem function. There is ample evidence that ecological responses to contemporary climate change are already occurring. In the Northern Hemisphere, many taxa show a consistent trend of northward or westward expansion of their ranges as well as altitudinal shifts (Thomas et al. 2001, Walther et al. 2002, Parmesan and Yohe 2003, Walther 2010). In Ontario, range expansions may increase biodiversity due to the introduction of new species in southern regions (Kerr and Packer 1998); however, range contractions and species loss are also likely to be prevalent across northern regions. Over the next century, the climate envelope of species may shift as much as 300 to 700 km north (Rizzo and Wiken 1992, McKenney et al. 2007). For example, the extent of the boreal forest bioclimatic envelope could be reduced by as much as 50%, with more southern areas being replaced by temperate bioclimatic envelopes (Rizzo and Wiken 1992, Malcolm et al. 2002, Gray 2005). Globally, rising temperatures have also caused the advancement of spring phenology (Root et al. 2003, Edwards and Richardson 2004, Parmesan 2006). As well, the introduction of southern competitors and pathogens (such as the Virginia opossum, *Didelphis virginiana*, and raccoon roundworm, *Baylisascaris procyonis*), increased extinction risk of cold-adapted species (such as the Canada lynx, *Lynx canadensis*, and American marten, *Martes americana*), and selection for early breeding (e.g., frog communities and muskrat, *Ondatra zibethicus*) have been noted (Pounds et al. 2006, Post and Forchhammer 2008, van der Wal et al. 2008, Bowman and Sadowski 2012). These changes appear to be systematic trends with considerable long-term consequences. In fact, it has been suggested that the effects of climate change on biodiversity will likely exceed the negative effects of habitat loss due to factors other than climate change such as urbanization (Sala et al. 2000, Thomas et al. 2004, Jetz et al. 2007).

Documentation of the effects of climate change in Ontario at the species level (e.g., range shifts) is progressing; however, extrapolating climate change research from populations to communities and ecosystems is difficult (Kareiva et al. 1993, Schmitz et al. 2003, Varrin et al. 2007, Tylianakis et al. 2008, Berg et al. 2010, Fenton and Spencer 2010). Climate change can amplify the effects of other major extinction drivers, such as habitat loss, disease, and invasive species. As well, species responses to climate change are connected through simultaneous interactions with other species or adjacent trophic levels (Harrington et al. 1999, Tylianakis et al. 2008, Van der Putten et al. 2010), and temporal and spatial overlap affect biotic interactions, both of which are highly influenced by climate variables (Walther et al. 2002). As such, complex networks of biotic interactions may be disrupted (Mora et al. 2007; Brooke et al. 2008), and synchrony in ecological systems (e.g., the lynx–hare cycle) may be reduced (Stenseth et al. 2002). However, the ability to anticipate biotic responses to climate change is limited to some degree by uncertainty about how species will respond, as well as how local climates will be affected by the complex, interactive effects of global changes (Houghton et al. 2001, Humphries et al. 2004, IPCC 2007). As such, predicting the effects of climate change on communities and species interactions is a challenge.

The single species effects of climate change were recently documented in the climate change research report entitled The Known and Potential Effects of Climate Change on Biodiversity in Ontario's Terrestrial Ecosystems (Varrin et al. 2007). Three general mechanisms that can affect species as a result of climate change were identified: demographic, phenological, and genetic, which can each result in either population expansions or contractions, depending on the ecology of particular species (Varrin et al. 2007). In addition to the species-specific effects of climate change, the potential effects of climate change on terrestrial communities remain of great concern. For example, long-standing species interactions and ecosystem services may be disrupted. As such, in this update of the review by Varrin et al. (2007), we have chosen to focus on the second part of that report, i.e., biotic interactions and the potential effects of climate change on terrestrial communities, as this is where the greatest uncertainty remains. Varrin et al. (2007) proposed four categories of climate change effects on biotic interactions: asymmetries, asynchronies, synergies, and thresholds. In this report, we elaborate on these topics with discussions of synergies, asynchrony, and asymmetry, and the outcome of these processes, i.e., community reassembly (Figure 2). We have omitted the threshold category as we believe thresholds can occur in all categories of community-level climate change effects (e.g., Folke et al. 2004). We begin with a brief review of the effects of climate on genetic change because we felt that recent research was sufficient to warrant an update of the information on this topic provided by Varrin et al. (2007).

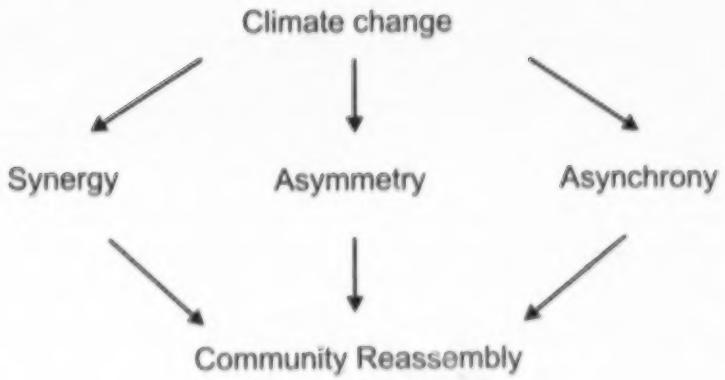

Figure 2. *A schematic depiction of the potential effects of climate change on communities. Classes of effects are synergy, asymmetry, and asynchrony, all of which can potentially culminate in community reassembly.*

We first summarize the potential genetic effects of climate change on terrestrial populations and communities, with a focus on wildlife. Second, we report on synergies between climate change and other extinction drivers, such as habitat fragmentation. Third, we discuss asynchronies and asymmetries between interacting species. And lastly, we discuss community reassembly, the outcome of these community-level climate change effects, and its resulting effects on species interactions. We also make recommendations for associated management considerations, research needs, and response strategies. In addition, we have included a glossary of technical terms (Appendix 1) used in this document, and an updated review of climate change studies of vertebrate species that occur in Ontario (Appendix 2). We updated the review by Varrin et al. (2007) by evaluating studies, including peer-reviewed journal articles or books published since 2006 inclusive, in which long-term data (>5 years) were quantitatively assessed for population responses to changing climate. Our review combined with that by Varrin et al. (2007) indicated that, overall, the longer-term effects of climate change have been studied on 181 species that occur in Ontario. Of these species, effects are reported as equivocal for 101, consistent with range expansion for 68, and consistent with range contraction for 12.

2.0 Genetic change

Summary

Climate change can initiate range expansions and contractions, changes in individual breeding behaviour, and population extinctions, all of which may significantly affect the genetic composition and structure of species, populations, and communities. The rapid northward expansion of some species may lead to increased secondary or renewed contact between species and populations resulting in increased incidence of hybridization. This may negatively affect species through loss of diversity and fitness declines, but positive effects are also possible, as in the hybrid vigour noted in recolonizing populations of fishers (*Martes pennanti*) in Ontario. Evidence also indicates that climate change can alter genetic connectivity among populations and many populations are predicted to decrease in size as a consequence of climate change, increasing the risk of losing genetic variation due to genetic drift.

When faced with new selection pressures caused by changing climate, species can disperse to suitable habitats elsewhere, accommodate the changes via phenotypic plasticity, adapt via genetic change, or face extinction. In the short-term, phenotypic change is likely to be a more important mechanism for coping with changing environmental conditions than evolutionary change; however, as climate change accelerates, plastic responses may be inadequate for providing long-term solutions to the challenges to species survival.

2.1 Adaptation

When faced with new selection pressures caused by a changing climate, species can disperse to suitable habitats elsewhere, adapt via phenotypic plasticity (without change in genotypes), adapt via genetic change (i.e., microevolution, a genetic response to consistent selection on heritable traits), or face extinction (Holt 1990,Visser 2008, Nicotra et al. 2010, Chen et al. 2011, Hoffmann and Sgro 2011).

Phenotypic plasticity, the ability of individuals to modify their behaviour, morphology, or physiology in response to altered environmental conditions, allows individuals to adapt to a rapidly changing environment (Walter et al. 2002, Price et al. 2003, Yeh and Price 2004). Phenotypic responses to climate change can include changes in behaviour (Visser et al. 2004, Jonzen et al. 2006, Both 2007), distribution (Parmesan 2006, Pounds et al. 2006, Hitch and Leberg 2007), and morphology (Yom-Tov 2001). Phenotypic changes allow organisms to cope with short-term environmental change; however, microevolution, which involves genetic modifications, is thought to be essential for the persistence of populations faced with long-term directional changes in the environment (Lande and Shannon 1996). Evidence indicates that such microevolutionary adaptation has occurred in several species in response to contemporary climate change. Réale et al. (2003) demonstrated that red squirrels (*Tamiasciurus hudsonicus*) in western Canada advanced breeding by 18 days over 10 years in response to warmer spring temperatures and increased spruce cone abundance. Part of this phenological change resulted from phenotypic plasticity (87%), but a smaller proportion of this shift resulted from genetic changes (13%), potentially representing a rapid evolutionary response to selective pressures resulting from climate change (Réale et al. 2003, Berteaux et al. 2004). As well, evolution towards greater dispersal has been documented in several species of insects. In the United Kingdom, two species of wing-dimorphic bush crickets (*Metrioptera roeselii*, *Conocephalus discolor*) have evolved longer wings at their northern range boundary, with mostly long-winged forms participating in a range expansion, while short-winged forms did not move farther north (Thomas et al. 2001).The relative influence of both plasticity and evolutionary adaptation on population persistence in a changing environment will likely depend on species characteristics such as generation time, mating system, dispersal capacity, the strength and direction of selection, and the presence of ecologically relevant genetic variation (Anderson et al. 2012). Overall though, ecological plasticity is likely to be more important than evolutionary change as a mechanism to cope with changing environmental conditions in the short-term, as plasticity acts within a generation, whereas evolutionary genetic changes involve multiple generations (Williams et al. 2008). However, there are limits to the extent of plastic responses, and they may be inadequate for providing long-term solutions to the challenges faced by species as climate change accelerates (Figure 3) (DeWitt et al. 1998, de Jong 2005).

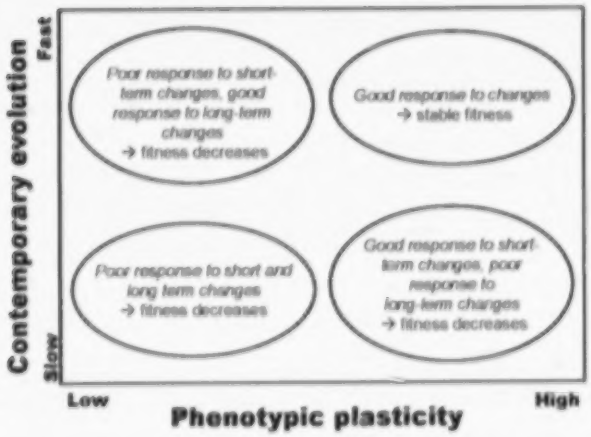

Figure 3. *Qualitative predictions of the response of a population to rapid environmental change (such as current and predicted climate change), based on the level of phenotypic plasticity and rate of contemporary evolution in the population (redrawn with permission after Berteaux et al. 2004).*

2.2 Population size and inbreeding

Evidence indicates that climate change can alter genetic connectivity among populations and as a result many populations are predicted to decrease in size (Møller et al. 2004). Smaller population sizes and reduced gene flow will most likely lower effective population size, and thereby increase the risk of losing genetic variation due to genetic drift (Frankham 1999, Cobben et al. 2012).

In Yosemite National Park, USA, changes in genetic diversity for populations of two species of small mammals have been observed to differ in response to climate warming (Rubidge et al. 2011). The alpine chipmunk (*Tamius alpinus*) has retracted its elevational range upwards as a result of a 3 °C temperature increase over the last 100 years. Conversely, the closely related and ecologically similar lodgepole chipmunk (*T. speciosus*) maintained a stable elevational range over the same period. Between the two time periods, *T. alpinus* showed increased genetic subdivision and loss of overall genetic diversity, with a significant decline in average allelic richness. As well, only modern *T. alpinus* populations showed significant isolation by distance. In contrast, *T. speciosus* showed no significant changes in population structure, overall gene diversity, or richness. These results strongly support a climate-driven range contraction that has resulted in a loss of genetic diversity and increased local isolation for alpine chipmunk populations (Rubidge et al. 2011). As the climate continues to warm, these and other montane species are likely to further contract their elevational range, experiencing further losses of genetic diversity and population fragmentation (Epps et al. 2006, Moritz et al. 2008). Genetic diversity is important for mitigating climate change effects, and loss of genetic diversity may signal demographic collapse and reduced fitness (Spielman et al. 2004, Hoffmann and Sgro 2011).

Similar processes appear to be underway in Ontario. Since the 1970s, Canada lynx populations have contracted at their southern range edge by almost 200 km and current populations along the contracting edge exhibit lower genetic variability than core lynx populations. The proximate cause of reduced genetic variability at range edges appears to be warm winter temperatures, although changes in forest composition may also play a role (Koen et al. 2014. Small population sizes will also lead to increased risk of inbreeding and inbreeding depression (Rowley et al. 1993, Kruuk et al. 2002). A long-term study of red-cockaded woodpeckers (*Picoides borealis*) found that inbred females are not adjusting their egg-laying date as the climate warms and, as such, their time of breeding no longer coincides with optimal foraging conditions for prey, such as insect larvae (Schiegg et al. 2002). However, females that are not inbred are laying eggs earlier than before, exhibiting phenotypic plasticity. By unequally affecting inbred and non-inbred individuals, climate change may pose an additional threat to endangered species (Azevedo et al. 2000).

2.3 Hybridization

Global climate change can shift climate regimes, leading to species range shifts and possibly increased secondary contact between recently diverged species (Parmesan 2006). For example, during a series of warm winters between 1995 and 2003, the southern flying squirrel (*Glaucomys volans*), a specialist of eastern temperate deciduous forests, rapidly expanded its northern range limit by approximately 200 km (Bowman et al. 2005). The range expansion brought *G. volans* into increased sympatry with its boreal forest counterpart, the northern flying squirrel (*G. sabrinus*), and resulted in the formation of a new hybrid zone in central Ontario (Bowman et al. 2005, Garroway et al. 2010).

In Canada's western Arctic, grizzly bears (*Ursus arctos*) have been increasingly present in polar bear (*Ursus maritimus*) territory (Kelly et al. 2010). Wild polar–grizzly hybrids and second-generation offspring have been documented in the northern Beaufort Sea of Arctic Canada (Miller et al. 2012). As the climate continues to warm, polar bears will likely be forced to spend increasingly more time on land due to the melting of the polar ice caps and shorter seasons of sea ice cover, perhaps even during the breeding season, bringing them into closer contact with grizzly bears (Miller et al. 2012). Similarly, interbreeding among other Arctic species could significantly affect polar biodiversity. For example, hybridization between the endangered North Pacific right whale and the more numerous bowhead whale could quickly push the former to extinction (Kelly et al. 2010). Lynx × bobcat (*Lynx rufus*) hybrids may occur in Ontario as the bobcat expands its range north, however these hybrids are expected to be relatively rare due to the relatively old divergence of this species pair; competition may be a more important process than hybridization in determining the effect of climate change on these two species (Bowman and Sadowski 2012).

Hybridization can be detrimental to species because of diversity loss, and fitness declines following admixture (Rhymer and Simberloff 1996, Muhlfeld et al. 2009). However, hybridization is one of the few mechanisms leading to new combinations of genes, which can facilitate evolutionary adaptation by introducing genetic variation (Hoffmann and Sgro 2011). For example, interspecies hybridization in Darwin's finches has introduced the genetic variance in morphology needed for adapting to changing climate conditions (Grant and Grant 2010). Meanwhile, in Ontario, fishers appear to exhibit hybrid vigour between recolonizing populations (Carr et al. 2007b). Therefore, as species range shifts occur and the incidence of hybridization increases, there may be unexpected evolutionary consequences and even benefits, such as improving adaptive capacity, when new variation is introduced into populations (Hoffmann and Sgro 2011).

3.0 Synergy

Summary

A synergy is an interaction of processes such that the total effect is greater than each process acting independently. The synergistic effects of habitat fragmentation, habitat loss, and climate change are expected to contribute to the decline of biological diversity. Populations in fragmented landscapes are more susceptible to environmental stressors, such as climate change, than those in connected landscapes. Habitat fragmentation increases isolation between populated habitats, and reduces population connectivity, which in turn increases the risk of extinction. Regions of Ontario with the most intensive land uses and the greatest level of landscape fragmentation, such as southern Ontario which is also the most biologically diverse area of the province, are particularly at risk. Similar synergies may occur between climate change and pathogens, whereby climate change facilitates the spread and effect of novel pathogens, and between climate change and invasive species.

3.1 Habitat loss and fragmentation

Habitat loss and fragmentation are two of the primary drivers of contemporary species extinctions (Mainka and Howard 2010). When habitat loss occurs, populations are at increased risk of extinction (Bender et al. 1994, Fahrig 2001). Furthermore, habitat fragmentation increases isolation between habitats, reducing population connectivity (Opdam 1991, Debinski and Holt 2000). Lack of connectivity, in turn, leads to reduced recolonization of locally extinct habitat patches, further increasing the probability of extinction over time across the whole landscape or metapopulation (Brown and Kodric-Brown 1977, Hanski and Gilpin 1991). Significant changes in species' populations and distributions have already been detected in response to the effects of each of these processes acting independently (Fahrig 2003). However, growing evidence suggests that the synergistic effects of habitat fragmentation, habitat loss, and climate change will also contribute significantly to the decline of biological diversity (Opdam and Wascher 2004, McLaughlin et al. 2005, Brooke et al. 2008), and the potential combined effects of these processes may be greater than those estimated individually (de Chazal and Rounsevell 2009).

Populations in fragmented landscapes are more susceptible to environmental stressors, such as climate change, than those in continuous landscapes (Meffe and Carroll 1997, Travis 2003). Yet climate change studies often presume that other habitat features in the environment are uniform; therefore, shifts in species geographic range are attributed to climate, while effects of landscape composition and configuration are not accounted for (Opdam and Wascher 2004). However, the assumption of uniform habitat does not hold true for many parts of Canada, where the most intensive land uses and the greatest level of landscape fragmentation are concentrated in biodiversity hotspots, such as southern Ontario (Kerr and Cihlar 2003). In today's anthropocentric world, areas of unsuitable landscape and man-made barriers such as highways, agricultural zones, and cities may impede species' movements. The resulting barriers to population connectivity among habitat patches will likely decrease dispersal (Wasserman et al. 2012), increase mortality (Fahrig et al. 1995), reduce genetic diversity (Reh and Seitz 1990, Wasserman et al. 2012), reduce recolonization following local extinction (Semlitsch and Bodie 1998), and may ultimately lead to population declines (Brown and Kodric-Brown 1977). For example, a rapid population decline of the green salamander (*Aneides aeneus*) within a highly fragmented habitat in the southern Appalachians, USA, has been linked to an increase in temperatures over the last 50 years (Corser 2001). As well, it is predicted that by the year 2100 as many as 1800 of the world's land bird species could be threatened by the synergistic effects of climate change and land conversion (Jetz et al. 2007).

Species' distributions are limited by bioenergetic constraints, suggesting that global warming will allow many species to expand northwards (Humphries et al. 2002). Theoretically, population expansion should be fastest in regions where landscape structure enhances dispersal, and should lag behind in regions where landscapes are fragmented. Warren et al. (2001) found that a butterfly range expansion in the United Kingdom did not occur in heavily fragmented landscapes. In spite of the improved habitat availability caused by climate warming, 93% of the butterfly species with small dispersal capacities declined, while most of the

species that did expand their ranges had large dispersal capacity. They concluded that the negative effect of habitat fragmentation on species distribution was overshadowed by the positive effect of a warmer climate. In general, we should expect asymmetric selection for species with good dispersal ability over those with poor dispersal ability (Kotiaho et al. 2005), and the synergy between habitat loss and habitat fragmentation will likely magnify this effect. In Ontario, the northward range expansion of both the hooded warbler (*Wilsonia citrina*) and the southern flying squirrel appears to have been simultaneously facilitated by climate warming and limited by habitat fragmentation (Bowman et al. 2005, Melles et al. 2011).

Habitat fragmentation can be caused by natural disturbances (Opdam and Wiens 2002). Some species have adapted to unpredictable habitat availability by developing high mobility, and consequently are less susceptible to human-induced fragmentation. These include species from coastal habitats and early successional stages of ecosystems as well as the boreal forests of Ontario, where many species have adapted to fire disturbance. Conversely, species in systems with relatively stable natural dynamics, such as tropical rain forests, have evolved under fairly predictable conditions in a more or less continuous habitat and are therefore likely to be more susceptible to fragmentation (Opdam and Wascher 2004). Moreover, the effect of fragmentation will vary among ecosystem types. Some have argued that fragmentation effects should be strongest at high levels of habitat loss (Fahrig 1997, Swift and Hannon 2010). Forests, grasslands, and wetlands often become highly fragmented with habitat loss, whereas shrublands, farmland, and pastures are regarded as less vulnerable (Mantyka-Pringle et al. 2012). As such, forests, grasslands, and wetlands, and the species that occur within them, are likely to be vulnerable to the synergistic effects of habitat conversion and climate change. Some positive effects of the interaction between habitat fragmentation and climate change may also occur. For example, higher temperatures might result in areas that were unsuitable for colonization by certain plants to become habitable, resulting in patches added to the habitat network and the overall improvement of the spatial cohesion of some landscapes (Thomas et al. 1999).

As time progresses, landscapes dominated by human land use, such as southern Ontario, will likely continue to change due to increasing urbanization, agricultural development, and economic activity, causing further habitat fragmentation. In landscapes most vulnerable to the synergistic effects of climate change and fragmentation, the development of ecological connectivity zones, networks of narrow corridors, and wildlife passages may help to lessen the negative effects on some species (Wasserman et al. 2012).

Case study: Marten

The American marten is associated with extensive snow pack, older forests, and the distribution of a competitor, the fisher (Carroll 2007, Krohn et al. 1995). Snow allows the marten, with its small ratio of body mass to foot area, to gain a competitive advantage over sympatric carnivores and may also affect prey abundance and vulnerability (Krohn et al. 1995). Climate change is projected to result in increases in winter temperature in many areas, which is likely to result in a decrease in winter snowpack and migration of forest communities upward in latitude and elevation (IPCC 2007, Littell et al. 2011). All of these changes will disadvantage the marten. Marten also have large area requirements, and thus are expected to be vulnerable to landscape change (Cardillo et al. 2006).

As such, climate change and its synergistic effects with habitat fragmentation are likely to affect American marten populations. Carroll (2007) examined these combined effects for marten in southeastern Canada and the northeastern United States, and found that marten populations showed stronger declines due to climate change alone than due to overharvest or logging, but climate change interacted with logging (which results in habitat loss and fragmentation) to increase overall vulnerability. This highlights the potential threats faced by small and semi-isolated populations, as climate change can interact with habitat conversion to form an extinction vortex (Carroll 2007, Gilpin and Soulé 1986).

3.2 Pathogens and parasites

Climate change can play a role in altering the dynamics and ecology of wildlife disease. Pathogens and their vectors are sensitive to changes in temperature, rainfall, and humidity (Harvell et al. 2002), thus climate warming can affect the distribution, seasonality, and severity of diseases (Le Conte and Navajas 2008).

Most pathogens and vectors, such as insects, have limited temperature and humidity ranges for survival and optimal reproduction. Indeed, many are limited by cold temperatures. Warmer temperatures could increase the incidence of disease both by increasing the vector population size and distribution, and by increasing the length of time vectors are present in the environment. If global temperatures, precipitation, and humidity rise, as is projected by climate change models (IPCC 2007), pathogens and vectors that are normally restricted to warmer, wetter, and lower altitude zones will be able to expand their range to previously inhospitable latitudes and altitudes leading to the exposure of naïve host populations (Kaeslin et al. 2012).

Vector-borne diseases have been predicted to increase at higher latitudes and altitudes under warming temperatures (Kuhn et al. 2005, Ogden et al. 2006). Lyme disease, a bacteria spread by some species of ticks, is currently uncommon in Canada, where established populations of vectors are limited to southern Ontario, Nova Scotia, and British Columbia. However, models suggest that the geographic range of tick species that transmit Lyme disease may expand significantly due to climate change, with a northern expansion of about 200 km projected by the year 2020 (Figure 4; Ogden et al. 2006). This expansion would likely be due to longer growing seasons resulting from warmer temperatures and decreased tick mortality during milder winters (Lindgren and Gustafson 2001). Seasonal tick activity under climate change scenarios suggests endemic cycles of *Borrelia burgdorferi*, the causative agent of Lyme disease, will be maintained in newly established tick populations (Ogden et al. 2006). As well, transmission of the bacterium to humans is often increased when warmer temperatures in the early spring result in the overlap of feeding activity of nymphal (virus infected) and larval (uninfected) *Ixodes scapularis* ticks. Under these weather conditions, infection is more readily passed from infected ticks to uninfected ticks through small rodents. Because the viral infection is brief in tick-infested rodents, feeding of both stages of tick at the same time results in more infected larval ticks and greater risk for Lyme disease infection in humans (Gatewood et al. 2009). In North America, tick-borne diseases such as babesiosis, anaplasmoses, and Powassan encephalitis, as well as mosquito-borne diseases such as dengue and West Nile virus, may also expand their ranges if there is a northern expansion of vector populations (Epstein 2001, Greer et al. 2008).

Figure 4. *Projected upper temperature limits for Ixodes scapularis establishment in Canada. The graph shows the current upper geographic limits and projected limits for the 2020s, 2050s, and 2080s, assuming continuous population growth, regionally oriented economic development, and no reduction in greenhouse gas emissions. Modified, with permission, from Elsevier (Ogden et al. 2006 and Greer et al. 2008).*

Climate change is expected to increase the frequency of extreme weather events that affect disease cycles (de la Rocque et al. 2008). For example, in Africa, outbreaks of Rift Valley fever, a mosquito-borne disease, have been linked with incidences of higher seasonal rainfall. Many insect vectors have population booms associated with large amounts of rain, and the flooding that accompanies heavy rainfall can increase the spread of waterborne pathogens. Conversely, decreased rainfall and drought can result in animals congregating around limited food and water resources, thereby increasing population densities and possibly increasing pathogen and parasite transmission (Kaeslin et al. 2012).

Climate change may also affect the immune status of host animals due to heat or nutritional stress. If increased temperatures or extreme weather events limit the availability or abundance of food, animals may become more susceptible to heavy parasite loads and may experience increased exposure and susceptibility to pathogens (Kaeslin et al. 2012). For example, survival of the brain worm (*Parelaphostrongylus tenuis*) of white-tailed deer (*Odocoileus virginianus*) may have increased due to recent warmer temperatures and milder winters in the northcentral United States and southern Canada. The parasite, which overwinters as larvae in snails, causes neurological disease in moose (*Alces alces*) and caribou (*Rangifer tarandus*). Moose are already experiencing health repercussions (such as increased heart rate and weight loss) due to heat stress caused by recent climate warming (Lenarz et al. 2009), and may therefore be more at risk of contracting parasitic and infectious diseases (Murray et al. 2009). Similarly, amphibians suffering from climate change induced stresses, such as increased ultraviolet radiation, may be more susceptible to pathogens (Harvell et al. 2002).

Due to climate warming, southern species such as the grizzly bear, red fox (*Vulpes vulpes*), and white-tailed deer have shifted their ranges north towards the Arctic (Kaeslin et al. 2012). These southern species bring diseases for which their Arctic counterparts, such as polar bear, Arctic fox (*Vulpes lagopus*), and caribou, have no immunity. For example, brucellosis, a bacterial disease found in cattle, dogs, wild animals, and humans, has now been found in baleen whales (*Mysticeti* spp.) (Kaeslin et al. 2012). Meanwhile, since 1995, the geographic range of the lung parasite (*Parelaphostrongylus odocoilei*) of caribou has shifted northward from the Pacific coastal range of the United States to include Alaska, and from British Columbia, Canada, to include the Yukon and Northwest Territories (Hoberg et al. 2008). Warmer summer temperatures also now allow lung nematode (*Umingmakstrongylus pallikuukensis)* larvae, often found in muskoxen, to develop to the infectious stage within the intermediate host, the marsh slug (*Deroceras laeve*), at a rate that has reduced the parasite's life cycle from 2 years to 1 year (Kutz et al. 2005). This means that muskoxen are now exposed to an increased intensity of infection and are infected earlier in the season and at younger ages. The parasite can compromise the respiratory system, and thus can have adverse effects on muskoxen fecundity, predation rates, and survival (Kutz et al. 2001).

Climate-driven changes in habitat and resources may also force animals to shift their ranges or to alter their migration routes into new ecosystems where they may introduce or be exposed to novel pathogens (Kaeslin et al. 2012). Conversely, climate warming could make environmental conditions on breeding grounds more favourable for year-round survival, replacing migratory populations with year-round resident populations (Lussenu et al. 2004, Bradshaw and Holzapfel 2007). Migrations can be beneficial by allowing hosts to escape the continual build-up of pathogens in the environment (Loehle 1995, Altizer et al. 2003) or by eliminating infected animals from the population during arduous migrations (Gylfe et al. 2000, Bradley and Altizer 2005). Altered migration routes and range shifts could result in migratory animals encountering and transferring pathogens to previously naïve host populations, or themselves becoming exposed to novel infectious diseases. Pathogens introduced into previously unexposed host populations can spread quickly, cause high fatality rates, and lead to significant host population declines (Harvell et al. 2009).

The climate is changing at an unprecedented rate, altering physical and biological processes, including patterns of infectious disease. Climate change is expected to increase levels of infection, change the distribution of diseases and parasites, affect host population dynamics, and have cascading ecological, sociological, and economic effects. As well, changes in the distribution and abundance of diseases and parasites will have significant implications for natural resource agency programs and the public at large. As such, research and monitoring of wildlife diseases should be encouraged, so that both natural resource and public health agencies have time to prepare response strategies when diseases begin to spread into new areas.

3.3 Invasive species

Biological invasions occur when a species is introduced to a habitat or ecosystem where it is not native and subsequently becomes established. Invasive species can reduce biodiversity and alter the structure and function of entire ecosystems (MacDougall and Turkington 2005, Mainka and Howard 2010, Vila et al. 2010). As a result of these effects, biological invasions are an important threat to biodiversity and ecosystem services, and are considered one of the five largest threats to ecosystem integrity (MEA 2005).

Recent research suggests that climate change is likely to interact with and affect the distribution, spread, abundance, and effects of invasive species (Gritti et al. 2006). Climate change may influence invasive species and their effects on species, populations, and ecosystems in several ways. First, global warming could provide new opportunities for introductions to areas where, until recently, those species were not able to survive. Species introduced from warmer regions to temperate areas have, until recently, been constrained by growing seasons that were too short or winter temperatures that were too cold, which prevented them from becoming naturalized (Walther et al. 2009). With warmer temperatures, some species may be able to extend their reproductive period and expand their northern range limits (Walther et al. 2002). For example, a strong association between patterns of the emergence of the invasive gypsy moth (*Lymantria dispar)* and climatic suitability is evident in Ontario (Régnière et al. 2009). Records indicate a significant increase in the distribution of the invasive moth since 1980 during which time the climate has warmed. However, between 1992 and 1997, a temporary decline in climatic suitability occurred and resulted in a drastic reduction in the area defoliated by these moths. Since 1998, the warming trend has continued, and resultant defoliation is expected to threaten hardwood forest resources as climate change allows the gypsy moth to expand farther north and west. It is estimated that by 2050 the proportion of Canada's deciduous forests at risk of gypsy moth damage will grow from the current 15% to more than 75% (Régnière et al. 2009).

In addition to the removal of physiological constraints, climate change can also affect dispersal of species in various ways. For example, warmer nocturnal temperatures increase flight activity of invasive winter pine processionary moth (*Thaumetopoea pityocampa)* females, enabling them to disperse over greater distances (Battisti et al. 2006). As well, increasing temperatures could result in an additional generation of the invasive moth each year (Walther et al. 2002). Meanwhile, the historic range of the North American native mountain pine beetle (*Dendroctonus ponderosae*) has been limited by climate. However, as a result of increased warming at higher latitudes and altitudes, the beetle is able to complete a life cycle in one season rather than the typical two, allowing for more rapid range expansion into new environments (Logan and Powell 2001).

Invasive species can have major effects on the communities and ecosystems they invade, where they may dominate function or richness and transform ecosystem properties, which inevitably leads to changes in biological communities (Richardson et al. 2000, Vila et al. 2009). By definition, invasive species are typically successful and abundant, whereas many native species are rare and constrained. Invasive species also tend to have characteristics that differ from non-invasive species, which may provide them with a competitive advantage under warming climatic conditions, and allow them to take over empty niches, or compromise native species' ability to compete against hardy generalist invaders (Mainka and Howard 2010). For example, many invasive plants have broad climatic tolerances and large geographic ranges, and also often have characteristics that facilitate rapid range shifts, such as low seed mass and short time to maturity (Rejmánek and Richardson 1996, Qian and Ricklefs 2006). Therefore, as the local environment changes, resident species may become increasingly poorly adapted, which will provide opportunities for newcomers that are better adapted and, thus, more competitive under the new conditions. For example, milder winters in central Europe changed the habitat of deciduous forests to conditions that are now more suitable for evergreen broad-leaved species (Berger et al. 2007). Acting together, climate change and invasive species can compromise the ability of many native species to survive, leading to reduced diversity of native species (Mainka and Howard 2010). These changes may subsequently alter existing species interactions, which may lead to unexpected effects on ecosystems (Tylianakis et al. 2008).

Finally, climate change may also challenge the definition of invasive species because in some areas species that were previously invasive may diminish in prevalence or effect. Meanwhile, native species may increase in abundance, and colonize new habitats taking on characteristics of exotic invaders (Hellman et al. 2008).

4. Asynchrony and asymmetry

Summary

Rapid climate change may reduce synchrony in co-evolved systems and may have asymmetric effects, which depend on species traits. Already, the phenology and distribution of many plant and animal species have changed, from the level of individuals to communities and across multiple trophic levels. The timing of events such as leaf unfolding, flowering, emergence of nymphs, arrival of migratory birds and butterflies, and breeding has advanced, whereas other events such as leaf fall have become delayed, leading to an extended growing season. Estimates are that 62% of species, most of which occur in the Northern Hemisphere, have already shifted their timing of spring events in response to recent climate warming. Variation in species' responses to climate change can alter existing relationships, resulting in asynchrony (or a mismatch) in predator-prey interactions, insect–plant interactions, migrations, reproduction, and phenology. For example, North American wood warblers (Parulidae) are not advancing in phenology in response to climate change as fast as key prey (such as the eastern spruce budworm, *Choristoneura fumiferana)*. As well, the iconic lynx–snowshoe hare (*Lepus americanus*) cycle may become decoupled as the climate warms. In general, the more specialized the relationship between species (e.g., plants and their pollinators), the more vulnerable each of them is likely to be to the phenological effects of climate change. Mistiming and mismatching can reduce individual fitness and result in population declines, increasing the risk of population extinctions and associated loss of biodiversity, while the decoupling of predator–prey relationships will likely affect other trophic levels.

Variation in species' responses to climate change can alter existing relationships, resulting in asynchrony (or a mismatch) in predator–prey interactions, insect–plant interactions, migrations, reproduction, and phenology. For example, in recent years the strong trophic interaction between winter moth (*Operophtera brumata*) egg hatching and English oak (*Quercus robur*) bud burst has begun to break down due to warming temperatures (Visser and Holleman 2001). In warm springs, winter moth eggs were predicted to hatch up to three weeks before oak buds burst. However, newly hatched caterpillars can only survive for a maximum of 10 days without food (Wint 1983), therefore asynchrony in this relationship can lead to increased mortality in winter moths (Visser and Holleman 2001).

Climate change could also alter the timing of predation events (e.g., prey and predator encounters), which could result in stronger or weaker trophic interactions between predators and prey (Møller et al. 2010). For example in Britain, newts (*Triturus* spp.) have advanced the timing of their entry into ponds, whereas their prey, the common frog (*Rana temporaria*), have not substantially altered their reproductive phenology (Beebee 1995). Therefore, embryos and larvae of early breeding frogs are now exposed to higher levels of newt predation (Walther et al. 2002). In Canada, the most iconic synchronous system is the cycle between Canada lynx and snowshoe hare, which is controlled, in part, by the influence of the NAO (North Atlantic Oscillation) (Stenseth et al. 2002). As specialized hunters, Canada lynx prey almost exclusively on snowshoe hare, and lynx populations are closely tied to population cycles of snowshoe hare. Synchrony between lynx and hare is greatest during cold periods, and synchrony appears to break down during periods of warming (Scott and Craine 1993). Canada lynx are highly effective deep snow hunters, therefore this pattern may be due, in part, to an increase in specialized predation during cold periods as a result of changes in snow depth and structure (Stenseth et al. 2004). As well, deep snow typically excludes the lynx's main competitors, the coyote (*Canis latrans*), fisher, and bobcat, from its winter habitat (Smith 1984, Litvaitis 1992, Murray et al. 1994, Krohn et al. 1995). Less snow cover could therefore mean more competition for lynx resulting from more predation on hares by other carnivores. Bobcats, coyotes, and fishers, who prey on a more diverse range of prey, may be better equipped to adapt to a changing climate than specialists such as the Canada lynx. As such, the lynx–snowshoe hare cycle may become decoupled as the climate warms (Stenseth et al. 2002, 2004).

Interspecific competition is one of the major factors determining the distribution and abundance of species and thus species composition at the community level as well (MacArthur and Levins 1967). In a stable environment, competition between two species over common resources should lead to niche differentiation or local

extinction of the weaker competitor (Hardin 1960). Changes in environmental conditions can affect the competitive relationships among species. For example, migratory bird species may be at a disadvantage compared to resident bird species because changes in their wintering areas and along migration routes do not necessarily reflect those occurring in their breeding areas (Berthold et al. 1998). Both resident and migratory species may be able to adapt to changes through selection, but individuals of resident species are expected to be better able to adjust to warming spring temperatures and an advanced phenology of their food items (Ahola et al. 2007).

Species that migrate from wintering grounds to breeding areas may also be more vulnerable to the effects of climate change because they may arrive at an inappropriate time to exploit the habitat optimally, may experience higher competition with resident species, and are involved in more inter-specific interactions that may be disrupted (Berthold et al. 1998, Lemoine and Böhning-Gaese 2003). Species of birds that migrate over long distances must co-occur with their food sources (while avoiding their enemies) in the habitat in which they grow, and then, following migration to their breeding grounds, egg-hatching must be in synchrony with the food sources that they feed to their newborns (Sillett et al. 2000). Short-distance migrants may be more flexible in their response to climate change, because the circumstances on their wintering grounds will be a better predictor for the optimal arrival time on their breeding grounds (Berthold et al. 1992, Pulido et al. 1996). For example, competition for nest-holes between resident great tits (*Parus major*) and migratory pied flycatchers (*Ficedula hypoleuca*) increases when the timing of breeding onset is closer to overlapping and when the densities of tits or pied flycatchers are high. All these factors can be affected by climate change, indicating that it has great potential to affect the level of interspecific competition between these two species (Ahola et al. 2007).

In another example, Adélie (*Pygoscelis adeliae*), gentoo (*P. papua*), and chinstrap (*P. antarcticus*) penguins in the Western Antarctic Peninsula breed in sequence and over a period of three weeks or less (Trivelpiece et al. 1987). This staggered breeding may reduce direct foraging competition during chick rearing (Lishman 1985, Trivelpiece et al. 1987), and is an important factor for the distribution of limited nesting space, as gentoo and chinstrap penguins can out compete Adélies for available space in mixed colonies (Carlini et al. 2005, Sander et al. 2007). However, as the climate has warmed, gentoo penguins have exhibited greater plasticity in breeding phenology, which has decreased the mean interval between Adélie and gentoo breeding in warm years, increasing competition for nesting space in mixed colonies (Lynch et al. 2012). This may be one explanation for why small Adélie populations breeding in mixed colonies with gentoo penguins have been declining in recent years (Lynch et al. 2008). As such, differential responses in breeding phenology to changing temperatures represent an additional mechanism by which climate change may affect competitive interactions (Lynch et al. 2012).

Phenology refers to the timing of plant and animal life cycle events and how these are influenced by seasonal and interannual variations in climate (Walther et al. 2002). The phenology of organisms has evolved through natural selection to match their environmental conditions and to maximize the fitness of individuals (Futuyma 1998). Under normal conditions, the timing of recurring activities in the dependent species is controlled by abiotic variables (such as temperature) such that synchronization is maintained (Visser and Holleman 2001). These response mechanisms are the result of selection under the range of conditions experienced in the past (van Noordwijk and Müller 1994). However, under novel environmental conditions, synchronization between different trophic levels can break down because natural selection on species cannot always keep pace with the rate of change in environmental conditions in a rapidly warming climate (Visser and Holleman 2001). Global warming has altered the phenology and distribution of many plant and animal species, resulting in changes from the level of individuals to communities and multiple trophic levels (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). The breakdown of phenological relationships will have important consequences for trophic interactions, food–web structures, predator–prey interactions, and biodiversity (Edwards and Richardson 2004). Climate warming has advanced the timing of events such as leaf unfolding (Menzel and Fabrian 1999), flowering (Fitter and Fitter 2002), emergence of nymphs (Roy and Sparks 2000), and breeding (Forchhammer et al. 1998, Dunn and Winkler 1999, Forchhammer et al. 2002), whereas other events such as leaf fall have become delayed, leading to an extended growing season for both plants and the species that feed on them (Menzel and Fabrian 1999).

Climate change has also affected the timing of avian migration (Inouye et al. 2000). If the phenology of a species is shifting at a different rate from that of the species on which it relies (i.e., for food or pollination), this will lead to

mistiming of its seasonal activities (Visser et al. 2004). In the Netherlands, the pied flycatcher is currently suffering a trophic mismatch with its insect prey. The timing of peak insect abundance has advanced with climate warming, however the birds are not arriving on their breeding grounds any earlier (Both and Visser 2001). As such, the birds are suffering from mistimed reproduction. Similarly, in response to increased temperatures and decreased spring snow cover, egg laying and hatching of the greater snow goose (*Chen caerulescens atlantica*) occurred progressively earlier over a 16-year period (Dickey et al. 2008). However, both gosling mass and size at fledging were lower and there was an overall decline in reproductive success, in part due to trophic mismatch between the hatching date of goslings and the timing of peak plant quality (Dickey et al. 2008). In the Rocky mountains, the American robin (*Turdus migratorius*) is now arriving 14 days earlier than it did 2 decades ago, but as there has been no advancement of the date of snow melt, the interval between the first arrival of the robins and the first date of bare ground (which correlates with food availability) has grown by 18 days over this period (Inouye et al. 2000).

Strode (2003) suggests that North American wood warblers are not advancing in phenology as fast as their key prey (such as the eastern spruce budworm, *Choristoneura fumiferana)* are responding to increased temperatures. The emergence of spruce budworm occurs at approximately the same time that buds flush on host trees (Candau and Fleming 2008). Earlier bud flush in some areas may facilitate spruce budworm outbreaks. As climate change progresses, frequency and duration of spruce budworm outbreaks is predicted to increase because of the positive effect of warmer winter and spring temperatures and drought on insect physiology (Greenbank 1963, Mattson and Haack 1987) and because of the possibility of reduced synchrony between the spruce budworm and its natural enemies, such as wood warblers (Fleming 2000). As such, a substantial increase in defoliation of trees is predicted for northern Ontario (Candau and Fleming 2008).

In general, the more specialized the relationship between species, the more vulnerable each of them is likely to be to the phenological effects of climate change. For example, if successful pollination of a particular plant requires a pollinator with very specific morphological characteristics (e.g., tongue length) (Corbet 2000), but that pollinator has advanced its phenology and is no longer present during peak flowering, then that plant is more vulnerable to losing these pollinator services than are species that are visited by a wide range of pollinator species. Climate change may affect co-occurrences of plant and pollinator species spatially as well as temporally. Range shifts in plants (e.g., Lenoir et al. 2008, Pompe et al. 2008, Thuiller et al. 2008) and pollinators (e.g., Parmesan 1996, Parmesan et al. 1999, Menéndez et al. 2007, Settele et al. 2008) are occurring, but overlaps in current species distribution may not persist. For example, Schweiger et al. (2008) modelled the climatic niche for the butterfly *Boloria titania* and its host plant *Polygonum bistorta* and found that the overlap of their climatic niches will be considerably reduced under projected climate change scenarios. However, while most incidences of asynchrony are expected to negatively affect the species involved, improved matching of beneficial interactions (e.g., pollination) or more mismatching of adverse interactions (e.g., release of a plant from its herbivore) may also occur (Visser and Holleman 2001).

Climate change is likely to disrupt existing species interactions by altering the temporal and spatial nature of events; however, the direction and magnitude of these shifts are difficult to predict. This difficulty arises because species and populations: (i) differ in the extent to which their life history events (such as breeding) are able to accelerate with warming, (ii) experience different warming trends due to variations in mean seasonal timing of events and microhabitat use, (iii) vary in the extent to which their phenological responses are driven/constrained by factors other than temperature, and (iv) may respond to changing climate in other ways, such as through distributional changes (Thackeray et al. 2010, Visser and Both 2005).

It has been estimated that 62% of species, most of which occur in the northern hemisphere, have already shifted their timing of spring events (such as earlier frog breeding, bird nesting, and arrival of migratory birds and butterflies) in response to recent climate warming (Parmesan and Yohe 2003), with different taxonomic groups and trophic levels showing different magnitudes of response (Parmesan 2007, Thackeray et al. 2010). As well, a significant number of species range shifts have been recorded (Parmesan and Yohe 2003, Walther et al. 2002). If species that rely on each other are indeed showing different magnitudes (or even directions) of response, then the implications may be severe for ecosystems, especially if keystone species are affected (Figure 5) (Winder and Schindler 2004, Visser and Both 2005).

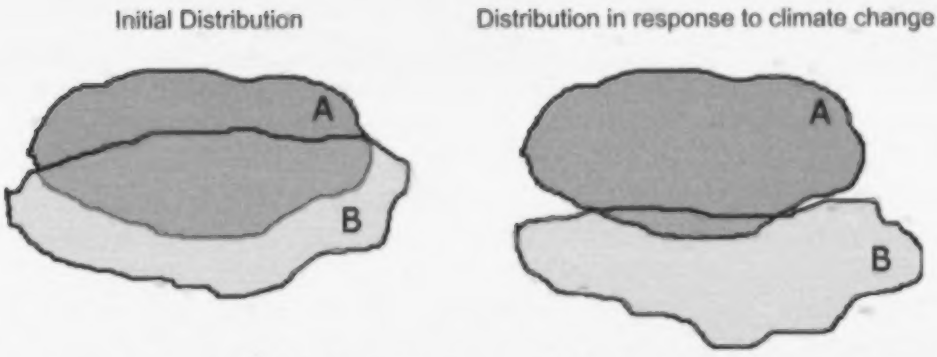

Figure 5. *Distribution of two species, A and B, whose ranges largely overlap, and species' distribution in response to climate change, where species-specific changes cause the ranges to separate. Adapted from Peters (1992).*

Such mistiming and mismatching has been linked to reductions in individual fitness and population declines, increasing the risk of population extinctions and biodiversity loss (Platt et al. 2003, Winder and Schindler 2004, Both et al. 2006, Miller et al. 2008). As well, the effects of the decoupling of predator–prey relationships will likely affect other trophic levels (Winder and Schindler 2004). As such, spatial and temporal mismatches can cause drastic ecological and economic consequences due to the influence of synchrony on processes such as pollination (Elzinga et al. 2007), fisheries production (Cushing 1990), and herbivory by agricultural pests (Harrington et al. 2007).

Case study: Caribou

Herbivores in the Arctic display seasonal reproduction that is timed to coincide with a peak in resource availability (Post 2003a, b). Caribou migrate between seasonal ranges and time their arrival on calving grounds to coincide with the timing of emergence of forage plants, which is crucial to the successful growth of newborn calves (Gunn and Skogland 1997). However, shifts in the timing of plant growth have already occurred at high latitudes, with plant emergence beginning earlier and lasting for a shorter period (Walther et al. 2002, Post 2003b, Forchhammer et al. 2005). As such, there is potential for a trophic mismatch between the timing of caribou arrival on their calving grounds and the timing of peak resource availability. Such a mismatch occurs when the timing of plant growth on breeding grounds advances due to warmer spring temperatures (Visser and Holleman 2001), while the timing of migration from wintering areas, which is cued by seasonal changes in day length, remains constant (Visser et al. 1998).This kind of trophic mismatch has already had negative consequences for caribou in west Greenland where temperatures have risen and forage plants have advanced their growing season by as much as 14.8 days, yet caribou calving has only advanced by 1.28 to 3.82 days, resulting in increased offspring mortality and a fourfold drop in offspring production (Post and Forchhammer 2008). As temperatures continue to warm throughout the Arctic, the extent to which plant phenology will further advance is a crucial factor in the future reproductive success of caribou (Post and Forchhammer 2008). In the Canadian High Arctic, a population of the endangered Peary caribou (*R. tarandus pearyi*) recently experienced a catastrophic and near-total population crash associated with increasing winter snow and ice crust formation (Miller and Gunn 2003). According to climate change projections, increasing snowfall and ice crust formation will continue to occur in this area as climate change progresses, further threatening the Peary caribou herd's future (Miller and Gunn 2003). In Ontario, climate change is expected to affect woodland caribou (*R. tarandus caribou*) through habitat loss (increased incidence and severity of fires), increased energy costs (as a result of summer heat and increased harassment by insects), and increased interaction with white-tailed deer (Racey 2004, Thompson and Baker 2007). As a result, woodland caribou may be restricted to a relatively small portion of northwestern Ontario (Thompson and Baker 2007).

5. Community reassembly

Summary

Individual species differ in their responses to climate change: some species will adapt, some cold-adapted species will leave communities, and some warm-adapted species may join communities, all resulting in the generation of novel biotic communities, referred to as community reassembly. Community reassembly can lead to changes in biodiversity, species interactions, trophic structure, and ecosystem processes and services. As well, community reassembly brings novel groups of species into contact, introduces new predators, new diseases, and new competitors into ecosystems, and can break down co-evolved species interactions. Community reassembly resulting from recent climate change has already been observed, including within several bird communities in Europe and North America. Many other changes are occurring or expected. For example, in Ontario, southern boreal forest tree species are expected to be gradually replaced by temperate forest species as summer temperatures warm, which will shift the dominant herbivore species within the deer family (Cervidae) from moose to white-tailed deer, with the effects potentially cascading to predator species.

The concepts we have discussed to this point, i.e., synergy, asynchrony, and asymmetry, will lead to the formation of novel ecological communities. This process, known as community reassembly, is already underway in Ontario. Community reassembly will have important consequences for biodiversity and ecosystem functioning.

Species assemblages are not fixed and novel interactions are a common occurrence in nature (Davis 1986, Vermeij 1991). The reassembly of communities has occurred frequently in history as a result of large-scale climate change events, such as when species recolonized much of North America after the last ice age. However, these changes were slower and of a smaller magnitude than contemporary changes (Quintero and Wiens 2013), which are expected to continue under current global climate change projections (Huntley et al. 1997, McLachlan et al. 2005). Individual species have different responses to climate change; some species will adjust via phenotypic plasticity, some will adapt via evolutionary change, some species will leave communities (via range shifts or local extinctions), and immigrating species may join communities, all resulting in the generation of novel biotic communities (community reassembly) (Møller et al. 2010). Community reassembly alters community composition and therefore can lead to changes in biodiversity, species interactions, trophic structure, and ecosystem processes (Barry et al. 1995, Fritts and Rodda 1998, D'Antonio and Vitousek 1992, Nussey et al. 2005). As well, community reassembly brings novel groups of species into contact, introduces new predators, new diseases, and new competitors into ecosystems, and can break down co-evolved species interactions (Morgan et al. 2004, Brooker et al. 2007). For example, the extinction of many vertebrates on the island of Guam is a result of their naïveté to a novel predator, the brown tree snake (*Boiga irregularis*), which invaded the community (Fritts and Rodda 1998).

Community reassembly resulting from recent climate change has already been observed within several bird communities (Lemoine et al. 2007, Stralberg et al. 2009, Virkkala and Rajasärkkä 2011). In Europe, climate change has altered the composition of bird communities, with an increase in the proportion of long-distance migratory species and a decrease in the proportion of short-distance migratory species (Lemoine et al. 2007). Similarly, Stralberg et al. (2009) assessed the potential changes in the composition of California's avian communities under future climate change scenarios. They suggested that by 2070, species range shifts may lead to dramatic changes in the composition of California's avian communities, such that as much as 57% of the state may be occupied by novel communities. In protected areas of Finland's boreal forest, northern bird species have declined by 21% and southern species increased by 29%, coinciding with a rise in mean temperatures, and leading to a change in boreal community structure (Virkkala and Rajasärkkä 2011). Climate changes also appear to have altered the bat communities of northern Costa Rica, as bat species are gradually colonizing higher elevations as the climate changes, and novel assemblages of bats now occur in the cloud forests (LaVal 2004).

In Ontario, southern boreal forest tree species are expected to be gradually replaced by temperate forest species as summer temperatures warm, thereby changing the structure of present-day boreal forest communities (Galatowitsch et al. 2009). As the southern boreal forest is replaced by temperate plant species, it is expected that many temperate fauna will shift north as well. For example, the dominant herbivore species within the deer family (Cervidae) will shift from moose to white-tailed deer, which are expected to become abundant across Ontario (Frelich et al. 2012), with potentially cascading effects on predator species, such as grey wolves (*Canis lupus*) and eastern wolves (*C. lycaon*), as well as on the community's food web as a whole, including other ungulate species such as caribou.

Community reassembly is expected to produce new and altered interactions among species (Tylianakis et al. 2007, 2008, Møller et al. 2010, Gilman et al. 2010). Species interactions can occur when their fundamental niches overlap (Schweiger et al. 2010), but not all interactions can be realized if the overlap of the fundamental niches of two species lies outside the current climate. However, as the climate changes, some of these interactions may become possible whereas others may disappear, changing the overall structure and functioning of communities (Schweiger et al. 2010).

Community reassembly may affect predator–prey interactions (a key process governing population dynamics; Murdoch et al. 2003) and modify fundamental food web properties (Møller et al. 2010). For example, community reassembly could be detrimental to predators if a specialist predator's prey shifts its range outside of the predator's community (Gilman et al. 2010). Conversely, reassembly might be beneficial to a species if it enables escape from antagonistic interactions, such as predation or competition. For example, species can benefit if they remain in their community while their predators and competitors shift their range to a new community (Menéndez et al. 2008, Van Grunsven et al. 2010). As well, if a novel prey expands its range into a new community, the prey base for predators in that community will increase (Gilman et al. 2010).

Individual plant and animal species will likely respond to climate change in different ways, shifting competitive balances to favour certain species over others (Tylianakis et al. 2008). Although novel species add to the species richness of a community upon their arrival, some can eventually cause the decline or even extinction of native species by out competing these species for limited resources, or via predation, disease, or replacement of resource species (D'Antonio and Dudley 1995, Dukes and Mooney 2004). Invading species often lack natural competitors or consumers and when released from their climatic constraints they can gain a competitive advantage in their expanded or introduced ranges thus significantly affecting communities (Dukes and Mooney 2004). For example, the red fire ant (*Solenopsis invicta*), an invasive species in the southern U.S., is extending its range north as the climate warms (Morrison et al. 2004). Invasive ants alter ecosystem processes by displacing native ant species that construct deep, long-lived nests rich in organic matter (MacMahon et al. 2000). As well, newly arriving competitors can take over available resources and prevent a later-arriving competitor from colonizing (Gilman et al. 2010).

With new species moving into communities, new diseases are expected to follow. Novel plants and animals can influence virus incidence in native species by introducing novel diseases and by increasing populations of vectors (D'Antonio and Meyerson 2002, Hampton et al. 2004, Malmstrom et al. 2005). The introduction of diseases to immunologically naïve hosts is often associated with increased prevalence and severity of disease (Bradley et al. 2005). *Echinococcus multilocularis* is a tapeworm that causes alveolar echinococcosis, a parasitic disease of canids and small rodents, which was previously unknown in northern Alaska (Bradley et al. 2005). The range expansion of the red fox to extreme northern Alaska may have had a role in the range expansion of *E. multilocularis* in brown lemmings (*Lemmus trimucronatus*) from the northern coast of Alaska (Bradley et al. 2005, Holt et al. 2005). *Baylisascaris procyonis*, a common roundworm of raccoons, is relatively harmless to raccoons, but can be fatal in rabbits, squirrels, groundhogs, other rodents, and humans (Kazacos 2001). Human infection by *B. procyonis* is an emerging health issue because raccoon populations are rapidly increasing, moving northward with climate change, and are living in close proximity to humans (Sorvillo et al. 2002, Bowman and Sadowski 2012). The parasite has been identified as one of the "deadly dozen" human pathogens thought to be affected by climate change (Wildlife Conservation Society 2008).

5.1 Breakdown of co-evolved interactions

Although many species interactions have a long evolutionary history, this synchrony may be lost due to the relative speed of today's anthropogenic climate change (Yurk and Powell 2009). Community reassembly is expected to disrupt co-evolved relationships between predators and their prey, plants and their pollinators, and others (Sherry et al. 2007; Tylianakis et al. 2007, 2008; Schweiger et al. 2010). In general, mutualistic interactions appear to be weakened by climate change (Tylianakis et al. 2008). For example, divergent range shifts in plants and pollinators are likely to change the amount of overlap in current species distribution, thereby disrupting mutualistic relationships (Schweiger et al. 2010). Changes in plant community composition and spatial mismatches in plant–pollinator responses to climate change may decrease pollinator availability for specialist plant species (Palmer et al. 2003). Similarly, Schweiger et al. (2008) modelled the climatic niche for the butterfly *Boloria titania* and its larval host plant *Polygonum bistorta* and found that the overlap of their climatic niches will be considerably reduced under future projected climate change scenarios, potentially disrupting this long-held trophic interaction. Walpole et al. (2012) demonstrated how unequal effects of increasing spring temperatures have led to an increase in the span of the breeding period for a community of anurans in Ontario. The asymmetric response by different anuran species may affect the type and strength of interspecific interactions (Donnelly and Crump 1998), and varying responses by species to climate change could alter the species composition of these communities and their fundamental ecological processes (Yang and Rudolf 2010).

5.2 Uncertainty

The long-term ecological consequences of community reassembly and the resulting interactions among previously unknown combinations of species are difficult to determine. Predicting the effects of community reassembly is problematic because we often lack sufficient data to fully determine how species will respond to climate change or to predict how novel species may interact with one another. As well, the numerous abiotic and biotic factors that are potentially susceptible to climate change, the differential sensitivities to changing conditions among species, and the complexity of species interactions, make species- and community-specific projections difficult (Tylianakis et al. 2007).

Biological communities will not move as a unit; instead, differing influences on individual species will cause them each to move in their own direction and at their own rate (i.e., asymmetrically). We can, therefore, anticipate that current communities will disassemble and the individual species will assemble into novel communities; however, the specific composition of these novel communities cannot be accurately predicted. As well, the order in which novel species colonize a community is important in determining community composition (Connell and Slatyer 1977), and the timing of species colonization can lead to alternative compositions (Diamond 1975). Further, although climate is a major determinant of species distributions (Pearson and Dawson 2003, Luoto et al. 2007), other factors, such as habitat fragmentation (Opdam and Wascher 2004, Schweiger et al. 2010, Mantyka-Pringle et al. 2012) and invasive species (Walther et al. 2009, Mainka and Howard 2010), will interact with climate change to affect species distributions and the formation of novel communities in ways that are difficult to predict (i.e., synergies). For example, Rempel (2012) demonstrated how the effects of climate change on moose populations will be complex, involving main effects and interactions among numerous variables, such as summer heat stress, winter tick-induced death, brain worm, and predation. Another major unknown is how the strength of already established interactions will change. If predators shift their diets to novel prey, the distribution of strong and weak interactions within food webs will be rearranged. In addition, it is uncertain what new species interactions will occur and how strong these interactions will be (Lurgi et al. 2012).

The novel communities that result from climate change may persist as species adapt or coexist, or they may undergo even further change as species are excluded through competition, predation, or other biotic interactions (Stralberg et al. 2009). Some range shifts are expected to have cascading effects on community structure and the functioning of ecosystems (Lovejoy and Hannah 2005). Nevertheless, novel communities will be characterized by high levels of ecological change, and ecosystem functioning may differ in ways that we cannot yet predict (Stralberg et al. 2009). As such, these novel ecosystems will present challenges and opportunities for conservation and management; therefore, we should attempt to formally incorporate uncertainty into climate change research and assessment processes.

5.3 Resilience

Ecosystem resilience is the ability of an ecosystem to withstand and absorb disturbances, and to recover to its pre-disturbance state without losing function and services (Holling 1996, Willams et al. 2008, Cote and Darling 2010). The concept includes two separate processes: resistance (the degree of disturbance that causes a change in state), and recovery (the speed of return to the original state) (Tilman and Downing 1994, Holling 1996, Cote and Darling 2010). Resilience may be a fundamental factor contributing to the sustained production of natural resources and ecosystem services in communities faced with uncertainty (Gunderson and Holling 2002). The life history traits that are predicted to promote resilience and reduce extinction risk include high reproductive rates, fast life history, and short life span (McKinney 1997). Resilience is also affected by the size of ecosystems, as small, fragmented habitats reduce the likelihood that species will be able to maintain a viable population size in the face of shrinking optimal habitats (Williams et al. 2008). Meanwhile, the ability to disperse within and across habitats, the ability to track preferred climate envelopes, and the ability to rapidly expand following disturbance will depend on both reproductive rates and dispersal ability (Fjerdingstad et al. 2007). The resilience of ecosystems to changing environmental conditions is also determined by the biological diversity and genetic variability of species within the ecosystem (Rejmánek 1996, Peterson et al. 1998, Wilmers et al. 2002). Communities with lower species diversity or those lacking keystone species (Paine 1969, Power et al. 1996) may be more vulnerable to the effects of climate change than communities with higher diversity. The impacts of current climate change, especially interacting with other pressures such as habitat fragmentation, might be sufficient to overcome the resilience of even some large areas of primary forests, transforming them into a permanently changed state. The resulting ecosystem state may be poorer in terms of both biological diversity and delivery of ecosystem goods and services (Thompson et al. 2009).

5.4 Regime shifts

The potential resilience of novel communities is generally unknown, although much research has been undertaken on this topic (Tilman and Downing 1994, Peterson et al. 1998). One common model argues that community resilience depends mostly on the number of species in the community (i.e., biodiversity; May 1973, Tilman 1999). Another model argues that resilience is an idiosyncratic product of the particular species present in the community (Lawton 1994).

In either case, the potential exists for 'regime shifts' to occur following community reassembly. Here, we define regime shifts after Folke et al. (2004), as alterations to ecosystem services that have consequent effects on human societies. A well-known example of a regime shift is a eutrophied lake, where high cyanobacteria counts and anoxic events lead to fish kills and a consequent loss of fishing opportunities (Folke et al. 2004). There is considerable potential for regime shifts in natural resources as a result of contemporary climate change (e.g., Chapin and Starfield 1997, Oosterkamp et al. 2000). As just one example, we are already seeing changes to furbearer distributions in the province that affect commercial fur harvesting activities (Koen et al. 2014). Widespread changes are also occurring in distributions of other animal and plant species (Varrin et al. 2007). It is likely that continued climate change will cause a variety of regime shifts in Ontario, altering socio-economically important ecosystem services. Regime shifts could occur as a gradual, continuous linear changes, or abruptly, as non-linear thresholds (Folke et al. 2004).

6. Recommendations

Summary

Given high uncertainty about future biodiversity in Ontario, we recommend implementing structured decision-making processes, such as adaptive management, that allow for learning through management activities to reduce future uncertainties. We also recommend that such research and management actions be integrated at appropriate spatial and temporal scales.

Resource managers in Ontario are faced with high uncertainty about the future composition of natural communities, and about the potential for deleterious regime shifts. Given these high levels of uncertainty, we recommend that decision-making processes be followed that allow for learning. Folke et al. (2004) argued that in the face of high uncertainty, resilience can be built into natural systems through management that is flexible and open to learning. Adaptive management is an example of a structured decision-making process that explicitly accommodates learning in the face of uncertainty. A key feature of the process is that management policies and actions are considered hypotheses that need to be evaluated and compared to alternative hypotheses. Therefore, the adaptive management process emphasizes creating and implementing different policy options to facilitate learning through decision making, thereby reducing uncertainty for future decisions. The learning process of adaptive management is often depicted as a loop (Figure 6).

There are many opportunities to integrate research and management activities to reduce future uncertainties about the effects of climate change on terrestrial biodiversity. To provide just one example, climate warming and competition with coyotes have both been posited as processes leading to reduced lynx abundance at southern latitudes (Ripple et al. 2011; Koen et al. 2014). These alternatives could be evaluated by manipulating coyote harvest while controlling for differences in climate, and vice versa. Such an experiment could be done at little financial cost by collecting routine management data.

We also recommend that research and management be applied and integrated at appropriate spatial and temporal scales. Given the large spatial scale of climate change, we expect that many of the biodiversity changes will occur at large scales, such as at the ecoregional level, and this should be recognized in the application of management decisions.

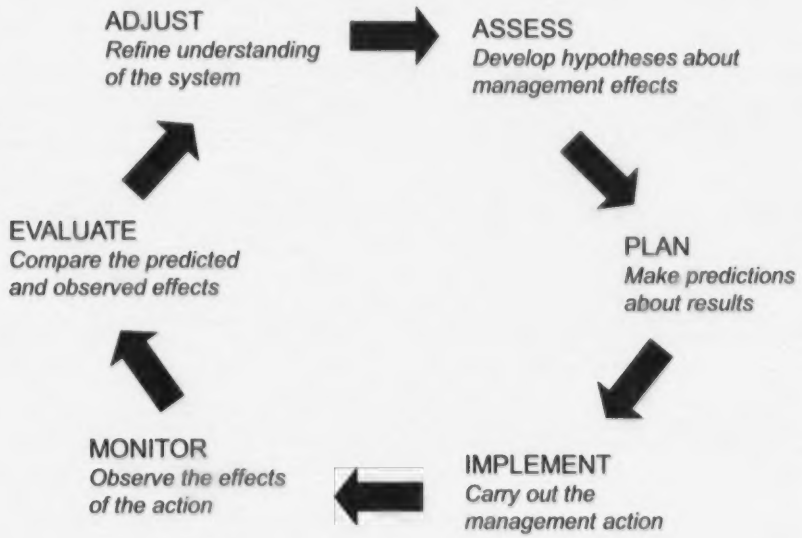

Figure 6. *A typical adaptive management loop. Adapted from Williams et al. (2009), and redrawn after MNR Risk Management (2013).*

We provide some specific suggestions for research and management activities below.

Research:

- Conduct research to fill knowledge gaps about species, biotic interactions, and community responses to climate change. Integrate research findings with management decision making.
- Due to the unpredictability of novel ecosystems, formally incorporate uncertainty into climate change research and assessment processes
- Develop integrated monitoring programs linked to management to help detect and verify change as it occurs. This will help to guide strategic decision making and calibrate future modelling efforts. Such integrated monitoring should be done as part of MNR's regular business.
- Undertake long-term studies that can separate genetic from plastic components of adaptive responses. Long-term studies are also an important tool for understanding ecosystem change.
- Research the mechanisms that confer community resilience to climate change (Williams et al. 2008).
- Identify species, populations, and communities that require active human intervention to mitigate losses.
- Develop models to better understand the complex potential outcomes of climate change on species, their interactions, and ecosystem functioning (Schmitz et al. 2003).
- Evaluate potential synergies between climate change and other stressors such as invasive species, habitat fragmentations, and disease (McCarty 2001, Opdam and Wascher 2004).
- Study genetic variability for fitness-related traits to identify species most at risk from climate change (Berteaux et al. 2004).
- Further investigate the role of biodiversity in ecosystem structure and function.
- Increase the monitoring of wildlife diseases and encourage collaboration between climate-change ecologists and infectious-disease researchers.

Management:

- Given uncertainty about the exact nature of ecosystem responses to climate change, embrace strategic flexibility, characterized by risk-taking (including decisions of no action), capacity to reassess conditions frequently, and willingness to change course as conditions change (Hobbs et al. 2006). Flexibility will increase manager's ability to deal with surprises as they occur (such as an insect pest suddenly switching from one generation per year to two generations per year, resulting in increased habitat damage).
- Accept different levels of uncertainty and risk associated with planning at regional scales relative to local scales (Saxon et al. 2005).
- Protect ecosystems with high biodiversity, especially those that maintain crucial components that may recover more easily from climatic disturbances, climate refugia, functional groups, keystone species, and multiple microhabitats within a biome.
- Maintain connectivity across forest landscapes by reducing fragmentation, recovering lost habitats (forest types), expanding protected area networks, and establishing buffer zones and ecological corridors (Thompson et al. 2009).
- Restore ecosystem function and maintain or preserve natural ecosystem processes with minimal human interference. Ecosystem-based adaptation may require giving priority to some ecosystem services at the expense of others.
- To promote ecosystem resilience, reduce and manage stresses faced by communities from other sources (such as habitat fragmentation, overharvest, invasive species, novel diseases) (Chapin et al. 2006). For example, minimize landscape fragmentation caused by road construction and urban development.
- Move from a focus on species towards a focus on communities and landscapes as conservation and management approaches are updated to incorporate climate change (Groves et al. 2012).

7. Conclusions

Over the next 100 years, the average annual temperature in Ontario is expected to increase by 5 °C, with greater increases in winter than summer temperature (IPCC 2007, McKenney et al. 2010). Precipitation is expected to increase, and extreme weather events, such as drought, rain, hail and ice, and windstorms are expected to increase in frequency (IPCC 2007). In general, weather is expected to become more variable under climate change.

These changes will add to the other pressures already affecting Ontario's biodiversity and ecosystem functioning. Although many species are thought to be able to cope with the direct effects of climate change, such as warming temperatures, indirect and interacting effects will likely play a larger role as climate change progresses (Callaghan et al. 2004, Luoto et al. 2007). Key drivers of these stresses are likely to be new synergistic interactions between climate change and other stressors, such as habitat loss, lack of connectivity, invasive species and disease, which are likely to constrain adaptive responses to climate change.

Globally, climate change is already significantly affecting species, biotic interactions, ecosystems, and the provision of ecosystem services. Changes in the timing of spring events (such as bud burst, flowering, migration, and breeding) have been widely documented (Parmesan and Yohe 2003, Root et al. 2003). Differing responses to climate change between interacting species has already resulted in increasing asynchrony in predator–prey and insect–plant systems,with mostly negative consequences, such as the decoupling of co-evolved species interactions between plants and their pollinators (Brooke et al. 2008, Post and Forchhammer 2008, Post et al. 2008). Species range shifts have also been well documented, as have expansions of warm-adapted communities (Chen et al. 2011, Hitch and Leberg 2007, Parmesan and Yohe 2003, Thomas et al. 2001). For example, species that were not historically adapted to Ontario's climate, such as the Virginia opossum, have already begun to shift their ranges north into the province. As well, climate warming is contributing to the continuing range expansion of white-tailed deer, but is expected to lead to range contractions of moose and woodland caribou. Meanwhile, Ontario's polar bear population, the southern-most population of polar bears in the world, may become extirpated within 45 years due to decreases in sea ice in Hudson Bay (Amstrup et al. 2007). Shifts in species distribution, phenology, abundance, and interactions can significantly alter community dynamics, leading to cascading effects throughout food webs and ecosystems (Coristine and Kerr 2011).

As well, invasive and non-native species, such as gypsy moth and mountain pine beetle, which were once restricted by colder winter temperatures, are expected to continue to spread at an increased rate (Mawdsley et al. 2009). Diseases and parasites (such as Lyme disease and raccoon roundworm) are also expected to spread, and shifts in abundances and ranges of parasites and their vectors are beginning to influence human disease dynamics (Pounds et al. 2006, van der Wal et al. 2008).

In southern Ontario and other areas with intensive land use and high levels of landscape fragmentation, the resulting barriers to population connectivity among habitat patches will likely affect species and communities through decreased dispersal (Wasserman et al. 2012), increased mortality (Fahrig et al. 1995), reduced genetic diversity (Reh and Seitz 1990, Wasserman et al. 2012), reduced recolonization following local extinction (Semlitsch and Bodie 1998), and ultimately may lead to population declines (Brown and Kodric-Brown 1977). Given that southern Ontario is one of the most species-rich areas of Canada, there is a clear need to escalate conservation efforts in these fragmented, human-dominated landscapes.

Although evolutionary responses to climate change have been documented, there is little evidence that observed genetic shifts would be able to prevent predicted species losses. Abiotic changes affect each species in a community differently because each species has its own physiological optimum and experiences climate conditions differently (Gilman et al. 2010). As such, rapid, anthropogenic climate change is ultimately causing the re-shuffling of communities as species respond according to their unique individual niche requirements and dispersal capacities (Coristine and Kerr 2011). New communities and ecosystems will appear, and lead to changes in species interactions at both the species and the ecosystem level, as well as to changes in the provision of ecosystem services.

Projecting community and ecosystem responses to climate change is one of the major challenges in modern ecology (Warren et al. 2001, McRae et al. 2008, Mora et al. 2007). Responses to climate change vary considerably, depending on the species, species interactions, synergies between pressures, and the spatial and temporal scale considered (de Chazal and Rounsevell 2009). Therefore, it is impossible to accurately predict future circumstances of all variables, and our understanding of the ecological effects of global change remains limited because community-level changes have been poorly documented, in part, due to the paucity of long-term data and the complexity of numerous interacting effects.

Incorporating climate change effects into resource management requires an understanding of the risks posed by climate change, not only to individual species, but to ecological communities, ecosystems, and resource users as well. Rapid climate change could impose novel demands on species and community-level conservation efforts. As such, this report was developed to update stakeholders on recent research on community-level effects of climate change to help identify potential climate change vulnerabilities, and to aid in developing climate change action plans, strategies, and policies. As well, our hope is that this report will stimulate further research on community-level climate change effects, consideration of methods for adaptation and mitigation, and implementation of structured decision making to reduce future uncertainties.

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Appendix 1: Glossary

A glossary of technical terms used in this report. Adapted from Ayala (1982), IPCC (2007), Varrin et al. (2007), Ricklefs (1990), and Sinclair et al. (2006).

Asynchrony	A discordance between or among processes.
Climate	The average weather conditions of a defined area over a long period of time.
Climate envelope	A description of the climate within which a species can persist; related to the fundamental niche.
Climate model	A quantitative description of the interactions between the atmosphere, oceans, and land surface. Best guesses about these interactions are used to forecast how changing CO_2 levels will affect a future world.
Community	A group of interacting populations.
Demography	The vital rates of a population; the study of the structure of a population.
Ecoregion	A unique area nested within one of Ontario's ecozones, defined by a characteristic range and pattern in climate, including temperature, precipitation, and humidity.
Hybridization	Successful interbreeding between two different species, subspecies, or populations.
Keystone species	Species that have a large environmental influence relative to their abundance.
North Atlantic Oscillation	A north-south alternation in atmospheric mass that has large-scale effects on weather.
Phenology	The study of the seasonality of animal and plant life.
Population	A group of individuals of a single species in a particular area.
Refugia	Locations of isolated or relict populations, where populations have persisted due to relatively benign conditions.
Regime shift	Alteration to ecosystem services that have consequent impacts on human societies.
Species richness	The number of different species in a defined area at a particular time.
Synergy	The interaction of two processes such that the total effect is greater than each process acting independently.
Uncertainty	An expression of the degree to which a value is unknown. It can result from lack of information or fromdisagreement about what is known or even knowable.
Weather	The condition of the atmosphere over a short period of time, as described by various meteorological phenomena.

Appendix 2: Summary of studies

A summary of studies of climate change effects on vertebrate species that occur in Ontario. Effects on the studied population(s) are noted as expansion, contraction, or equivocal. Studies include peer-reviewed journal articles or books in which long-term data (>5 years) were quantitively assessed for population responses to changing climate. Some additional studies were included if they were relevant to Ontario. Responses of vertebrate species that occur in Ontario but are not listed in the table were not found in the published literature. Of the 181 species listed in the table, reported effects are equivocal for 102, are consistent with expansion for 68, and are consistent with contraction for 11.

Class	Common name	Scientific name	Documented effects of climate change on the population	Comment	Sources
Amphibia	American Toad	*Bufo americanus*	EQUIVOCAL	Spring call initiation unchanged 1900-1912 to 1990-1999	Gibbs and Breisch 2001
Amphibia	Bullfrog	*Rana catesbeiana*	EXPANSION	Spring call initiation earlier in 1990-1999 compared to 1900-1912	Gibbs and Breisch 2001
Amphibia	Fowler's Toad*	*Bufo fowleri*	EQUIVOCAL	Spring call initiation unchanged 1980 to 1998	Blaustein et al. 2001
Amphibia	Gray Treefrog	*Hyla versicolor*	EXPANSION	Spring call initiation earlier in 1990-1999 compared to 1900-1911, expansion into Northern Ontario	Gibbs and Breisch 2001, Weller 2009
Amphibia	Green Frog	*Rana clamitans*	EQUIVOCAL	Spring call initiation unchanged 1900-1912 to 1990-1999	Gibbs and Breisch 2001
Amphibia	Northern Leopard Frog	*Rana pipiens*	EXPANSION	Calling influenced by spring temperatures (1995-2008)	Walpole et al. 2012
Amphibia	Red-backed Salamander	*Plethodon cinereus*	EQUIVOCAL	Leadback morph becoming more common, associated with warmer temperatures	Gibbs and Karraker 2005
Amphibia	Spring Peeper	*Pseudacris crucifer*	EQUIVOCAL	Breeds earlier in warmer years	Blaustein et al. 2001, Gibbs and Breisch 2001
Amphibia	Wood Frog	*Rana sylvatica*	EXPANSION	Spring call initiation earlier in 1990-1999 compared to 1900-1912, calling influenced by spring temperatures (1995-2008)	Gibbs and Breisch 2001, Walpole 2012
Reptilia	Painted Turtle	*Chrysemys picta*	CONTRACTION	Temperature-dependent sex determination; grow larger and reach maturity quicker during warmer sets of years	Janzen 1994, Frazer et al. 1993
Aves	Alder Flycatcher	*Empidonax alnorum*	CONTRACTION	Spring arrival date became later 1899-1911 to 1994-1997	Wilson et al. 2000

Aves	American Bittern	*Botaurus lentiginosus*	EQUIVOCAL	Spring arrival date in Maine unchanged 1899-1911 to 1994-1997; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	American Coot	*Fulica americana*	EXPANSION	Spring arrival is advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	American Kestrel	*Falco sparverius*	EQUIVOCAL	Spring arrival is unrelated to temperature in Manitoba	Murphy-Klassen et al. 2005
Aves	American Redstart	*Setophaga ruticilla*	EQUIVOCAL	Spring arrival is later in Maine; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	American Robin	*Turdus migratorius*	EQUIVOCAL	Spring arrival is earlier in parts of its range, not in others; lays eggs earlier in warmer springs; spring arrival is advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Torti and Dunn 2005,Inouye et al. 2000, Wilson et al. 2000, Bradley et al. 1999
Aves	American Woodcock	*Scolopax minor*	EXPANSION	Spring arrival is earlier in parts of its range; calling earlier	Butler 2003, Wilson et al. 2000, Bradley et al. 1999
Aves	Bald Eagle*	*Haliaeetus leucocephalus*	EXPANSION	Documented population increase	Ritchie and Ambrose 1996
Aves	Baltimore Oriole	*Icterus galbula*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997 in Maine; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Bank Swallow	*Riparia riparia*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Barn Swallow*	*Hirundo rustica*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later or unchanged in others; clutch size increase	Butler 2003, Wilson et al. 2000
Aves	Bay-breasted Warbler	*Dendroica castanea*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Belted Kingfisher	*Ceryle alcyon*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000, Bradley et al. 1999,
Aves	Black-and-white Warbler	*Mniotilta varia*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Black-billed Cuckoo	*Coccyzus erythropthalmus*	EQUIVOCAL	Spring arrival became later 1899-1911 to 1994-1997,276 km northward range expansion 1967-1971 to 1998-2002	Wilson et al. 2000, Hitch and Leberg 2007

Aves	Blackburnian Warbler	*Dendroica fusca*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in others	Butler 2003, Wilson et al. 2000
Aves	Black-capped Chickadee	*Poecile atricapillus*	CONTRACTION	Hybridization with Carolina chickadees whose range is expanding	Curry 2005
Aves	Black-crowned Night-Heron	*Nycticorax nycticorax*	EQUIVOCAL	Spring arrival in Manitoba is unrelated to temperature	Murphy-Klassen et al. 2005
Aves	Blackpoll Warbler	*Dendroica striata*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Black-throated Blue Warbler	*Dendroica caerulescens*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Black-throated Green Warbler	*Dendroica virens*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Blue-gray Gnatcatcher	*Polioptila caerulea*	EXPANSION	314 kmnorthward range expansion 1967-1971 to 1998-2002	Hitch and Leberg 2007
Aves	Blue-headed Vireo	*Vireo solitarius*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Blue-winged Warbler	*Vermivora pinus*	EXPANSION	Spring arrival is earlier in some parts of its range; 85 km northward range expansion 1967-1971 to 1998-2002	Hitch and Leberg 2007, Butler 2003
Aves	Bobolink*	*Dolichonyx oryzivorus*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in others; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Broad-winged Hawk	*Buteo platypterus*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Brown Creeper	*Certhia familiaris*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Brown Thrasher	*Toxostomum rufum*	EQUIVOCAL	Spring arrival is earlier in parts of its range, not in others; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000, Bradley et al. 1999
Aves	Brown-headed Cowbird	*Molothrus ater*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Canada Goose	*Branta canadensis*	EXPANSION	Onset of nesting earlier; spring arrival in Manitoba is advancing with warming temperatures	Murphy-Klassen et al. 2005, MacInnes et al. 1990
Aves	Canada Warbler*	*Wilsonia canadensis*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000

Aves	Cape May Warbler	*Dendroica tigrina*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Cardinal	*Cardinaalis cardinalis*	EXPANSION	Calling earlier	Bradley et al. 1999
Aves	Chestnut-sided Warbler	*Dendroica pensylvanica*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Chimney Swift*	*Chaetura pelagica*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in others	Butler 2003, Wilson et al. 2000
Aves	Chipping Sparrow	*Spizella passerina*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Chuck-will's-widow	*Caprimulgus carolinensis*	EQUIVOCAL	No significant range shift 1967-1971 to 1998-2002	Hitch and Leberg 2007
Aves	Clay-coloured Sparrow	*Spizella pallida*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Cliff Swallow	*Petrochelidon pyrrhonota*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Common Grackle	*Quiscalus quiscula*	EXPANSION	Spring arrival advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Common Loon	*Gavia immer*	EXPANSION	Spring arrival became earlier 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Common Nighthawk*	*Chordeiles minor*	EQUIVOCAL	Spring arrival became later 1899-1911 to 1994-1997 in Maine; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Common Snipe	*Gallinago gallinago*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, not in others; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Common Yellow-throat	*Geothlypis trichas*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997 in Maine; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Cooper's Hawk	*Accipiter cooperii*	EXPANSION	Spring arrival in Manitoba is unrelated to temperature	Murphy-Klassen et al. 2005
Aves	Dark-eyed Junco	*Junco hyemalis*	EXPANSION	Spring arrival is advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Double-crested Cormorant	*Phalacrocorax auritus*	EXPANSION	Spring arrival in Manitoba is advancing with warming temperatures	Murphy-Klassen et al. 2005
Aves	Eastern Bluebird	*Sialia sialis*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in Maine; lays eggs 4 days earlier than in the 1970s	Torti and Dunn 2005, Butler 2003,Wilson et al. 2000, Bradley et al. 1999

Aves	Eastern Kingbird	*Tyrannus tyrannus*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997 in Maine; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Eastern Meadowlark*	*Sturnella magna*	EXPANSION	Spring arrival is earlier in some parts of its range	Bradley et al. 1999
Aves	Eastern Phoebe	*Sayornis phoebe*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in others; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Bradley et al. 1999
Aves	Eastern Wood-pewee	*Contopus virens*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Field Sparrow	*Spizella pusilla*	EQUIVOCAL	Spring arrival earlier in some parts of its range, later in others	Butler 2003, Wilson et al. 2000
Aves	Fox Sparrow	*Passerella iliaca*	EQUIVOCAL	Spring arrival earlier in parts of its range, unchanged in others; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Golden-winged Warbler*	*Vermivora chrysoptera*	EXPANSION	Spring arrival earlier in some parts of its range, 148 km northward range expansion 1967-1971 to 1998-2002	Butler 2003, Hitch and Leberg 2007
Aves	Gray Catbird	*Dumetella carolinensis*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Gray Jay	*Perisoreus canadensis*	CONTRACTION	Populations decline following warmer autumns possibly due to hoard rot	Waite and Strickland 2006
Aves	Gray-cheeked Thrush	*Catharus minimus*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Great Blue Heron	*Ardea herodias*	EXPANSION	Spring arrival is earlier in some parts of its range; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000, Bradley et al. 1999
Aves	Great Crested Flycatcher	Myiarchus crinitus	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Greater Yellowlegs	*Tringa melanoleuca*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Green Heron	*Butorides virescens*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Henslow's Sparrow*	*Ammodramus henslowii*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Hermit Thrush	*Catharus guttatus*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in others; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000

Aves	Hooded Warbler*	*Wilsonia citrina*	EXPANSION	115 km range expansion 1967-1971 to 1998-2002	Hitch and Leberg 2007
Aves	Horned Grebe*	*Podiceps auritus*	EXPANSION	Spring arrival is advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Horned Lark	*Eremophila alpestris*	EQUIVOCAL	Spring arrival is unrelated to temperature in Manitoba	Murphy-Klassen et al. 2005
Aves	House Wren	Troglodytes aedon	EQUIVOCAL	Spring arrival is earlier in some parts of its range; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Bradley et al. 1999
Aves	Ivory Gull	*Pagophila eburnea*	CONTRACTION	Observed population declines, Reduced sea ice	Mallory et al. 2003
Aves	Indigo Bunting	*Passerina cyanea*	EXPANSION	Spring arrival earlier in some parts of its range	Butler 2003, Wilson et al. 2000
Aves	Kentucky Warbler	*Oporornis formosus*	EXPANSION	148 km northward range expansion 1967-1971 to 1998-2002	Hitch and Leberg 2007
Aves	Killdeer	Charadrius vociferous	EXPANSION	Spring arrival is earlier in some parts of its range; lays earlier in warmer springs	Murphy-Klassen et al. 2005, Torti and Dunn 2005, Butler 2003
Aves	Kirtland's Warbler*	*Setophaga kirtlandii*	CONTRACTION	Habitat loss	Botkin et al. 1991
Aves	Least Flycatcher	*Empidonax minimus*	EQUIVOCAL	Spring arrival date became later 1899-1911 to 1994-1997 in Maine; unrelated to advancing temperature in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Least Sandpiper	*Calidris minutilla*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Lesser Yellowlegs	*Tringa flavipes*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Lincoln's Sparrow	*Melospiza lincolnii*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Louisiana Water-thrush*	*Seiurus motacilla*	EQUIVOCAL	Spring arrival is earlier in parts of its range and later in others; No significant range shift 1967-1971 to 1998-2002	Hitch and Leberg 2007, Butler 2003
Aves	Magnolia Warbler	*Dendroica magnolia*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in others	Butler 2003, Wilson et al. 2000
Aves	Marsh Wren	*Cistothorus palustris*	EQUIVOCAL	Spring arrival is earlier in some parts of its range; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003

Aves	Mourning Dove	*Zenaida macroura*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Mourning Warbler	*Oporornis philadelphia*	EQUIVOCAL	Spring arrival is earlier in parts of its range and later or unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Nashville Warbler	*Vermivora ruficapilla*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Northern Flicker	*Colaptes auratus*	EQUIVOCAL	Spring arrival became later 1899-1911 to 1994-1997 in Maine; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Northern Harrier	*Circus cyaneus*	EXPANSION	Spring arrival in Manitoba is advancing with warming temperatures	Murphy-Klassen et al. 2005
Aves	Northern Mocking-bird	*Mimus polyglottus*	EQUIVOCAL	No significant range shift 1967-1971 to 1998-2002	Hitch and Leberg 2007
Aves	Northern Parula	*Parula americana*	EQUIVOCAL	Spring arrival is later in some parts of its range, not in others	Butler 2003, Wilson et al. 2000
Aves	Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Northern Water-thrush	*Seiurus noveboracensis*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Olive-sided Flycatcher*	*Contopus cooperi*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Osprey	*Pandion haliaetus*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Ovenbird	*Seiurus aurocapillus*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Palm Warbler	*Dendroica palmarum*	EQUIVOCAL	Spring arrival is later in some parts of its range; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003
Aves	Pectoral Sandpiper	*Calidris melanotos*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Philadel-phia Vireo	*Vireo philadelphicus*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Pied-billed Grebe	*Podilymbus podiceps*	EXPANSION	Spring arrival in Manitoba is advancing with warming temperatures	Murphy-Klassen et al. 2005
Aves	Pine Warbler	*Dendroica pinus*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Prairie Warbler	*Dendroica discolor*	EQUIVOCAL	No significant range shift 1967-1971 to 1998-2002	Hitch and Leberg 2007
Aves	Purple Finch	*Carpodacus purpureus*	EXPANSION	Spring arrival advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005

Aves	Purple Martin	*Progne subis*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Red-eyed Vireo	*Vireo olivaceus*	EQUIVOCAL	Spring arrival earlier in parts of its range and later or unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Red-tailed Hawk	*Buteo jamaicensis*	EXPANSION	Spring arrival in Manitoba is unrelated to temperature	Murphy-Klassen et al. 2005
Aves	Red-winged Blackbird	*Agelaius phoeniceus*	EXPANSION	Spring arrival is earlier in parts of its range; lays eggs 7.5 days earlier; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Torti and Dunn 2005, Wilson et al. 2000, Bradley et al. 1999
Aves	Rose-breasted Grosbeak	*Pheuticus ludovicianus*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003, Wilson et al. 2000, Bradley et al. 1999
Aves	Ruby-crowned Kinglet	*Regulus calendula*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Ruby-throated Humming-bird	*Archilochus colubris*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003, Wilson et al. 2000
Aves	Rusty Blackbird*	*Euphagus carolinus*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Sandhill Crane	*Grus canadensis*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Savannah Sparrow	*Passerculus sandwichensis*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, later in others	Butler 2003, Wilson et al. 2000
Aves	Scarlet Tanager	*Piranga olivacea*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Semi-palmated Sandpiper	*Calidris pusilla*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Sharp-shinned Hawk	*Accipiter striatus*	EQUIVOCAL	Spring arrival in Manitoba is unrelated to temperature	Murphy-Klassen et al. 2005
Aves	Short-eared Owl*	*Asio flammeus*	EQUIVOCAL	Spring arrival is unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Snow Goose	*Chen caerulescens*	EQUIVOCAL	Onset of nesting earlier; spring arrival in Manitoba unrelated to temperature, reduction of some components of breeding success	Murphy-Klassen et al. 2005, MacInnes et al. 1990, Dickey et al. 2003
Aves	Solitary Sandpiper	*Tringa solitaria*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003

Aves	Song Sparrow	*Melospiza melodus*	EQUIVOCAL	Spring arrival became later 1899-1911 to 1994-1997 in Maine; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Sora	*Porzana carolina*	EQUIVOCAL	Spring arrival is earlier in some parts of its range; unrelated to advancing temperature in Manitoba	Murphy-Klassen et al. 2005, Butler 2003
Aves	Spotted Sandpiper	*Actitis macularia*	EXPANSION	Spring arrival is earlier in some parts of its range; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003
Aves	Summer Tanager	*Piranga rubra*	EXPANSION	43 km northward range expansion 1967-1971 to 1998-2002	Hitch & Leberg 2007
Aves	Swamp Sparrow	*Melospiza melodus*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Swainson's Thrush	*Catharus ustulatus*	EXPANSION	141 km northward range expansion 1967-1971 to 1998-2002	Hitch & Leberg 2007, Ruegg et al. 2006
Aves	Tennessee Warbler	*Vermivora peregrina*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003, Wilson et al. 2000
Aves	Towhee	*Pipilio erythrophthalamus*	EQUIVOCAL	Did not show earlier arrival	Wilson et al. 2000, Bradley et al. 1999
Aves	Tree Sparrow	*Spizella arborea*	EXPANSION	Spring arrival advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005
Aves	Tree Swallow	*Tachycineta bicolor*	EQUIVOCAL	Spring arrival is earlier some parts of its range; Average egg-laying date up to 9 days earlier across NA; not laying earlier at Long Point, Ontario where temperatures have not increased; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Hussell 2003, Wilson et al. 2000, Dunn and Winkler 1999
Aves	Turkey Vulture	*Cathartes aura*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Veery	*Catharus fuscescens*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Vesper Sparrow	*Pooecetes gramineus*	EQUIVOCAL	Spring arrival became later 1899-1911 to 1994-1997 in Maine; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Wilson et al. 2000
Aves	Virginia Rail	*Rallus limicola*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Warbling Vireo	*Vireo gilvus*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Whip-poor-will*	*Caprimulgus vociferus*	EXPANSION	Spring arrival is earlier in some parts of its range, later in others	Wilson et al. 2000, Bradley et al. 1999

Aves	White-crowned Sparrow	*Zonotrichia leucophrys*	EQUIVOCAL	Spring arrival is earlier in some parts of its range; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003
Aves	White-throated Sparrow	*Zonotrichia albicollis*	EQUIVOCAL	Spring arrival is earlier in some parts of its range; unrelated to warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Willow Flycatcher	*Empidonax traill*	EXPANSION	135 km northward range expansion 1967-1971 to 1998-2002	Hitch &Leberg 2007
Aves	Wilson's Warbler	*Wilsonia pusilla*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others; advancing with warming temperatures in Manitoba	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Winter Wren	*Troglodytes troglodytes*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Wood Duck	*Aix sponsa*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Wood Thrush	*Hylocichla mustelina*	EXPANSION	Spring arrival is earlier in some parts of its range	Bradley et al. 1999, Butler 2003
Aves	Yellow Palm Warbler	*Dendroica palmarum hypochrysea*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Yellow Warbler	*Dendroica petechia*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Yellow-bellied Flycatcher	*Empidonax flaviventris*	EQUIVOCAL	Spring arrival date unchanged 1899-1911 to 1994-1997	Wilson et al. 2000
Aves	Yellow-bellied Sapsucker	*Sphyrapicus varius*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Butler 2003, Wilson et al. 2000
Aves	Yellow-billed Cuckoo	*Coccyzus americanus*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Aves	Yellow-breasted Chat*	*Icteria virens*	EQUIVOCAL	No significant range shift 1967-1971 to 1998-2002	Hitch and Leberg 2007
Aves	Yellow-rumped Warbler	*Dendroica coronata*	EQUIVOCAL	Spring arrival is earlier in some parts of its range, unchanged in others	Murphy-Klassen et al. 2005, Butler 2003, Wilson et al. 2000
Aves	Yellow-throated Vireo	*Vireo flavifrons*	EXPANSION	Spring arrival is earlier in some parts of its range	Butler 2003
Mammalia	Arctic Fox	*Alopex lagopus*	CONTRACTION	Competition and predation by red foxes expanding north, changes in prey abundance, habitat loss	Selås and Vik 2007, Hersteinsson and Macdonald 1992
Mammalia	Caribou*	*Rangifer tarandus*	CONTRACTION	Reduced body weight of calves	Weladji and Holland 2003

Mammalia	Deer Mouse	*Peromyscus maniculatus*	EQUIVOCAL	No effect of climate on initiation of spring breeding 1985 to 2003, Range contraction	Millar and Herdman 2004, Myers et al. 2009
Mammalia	Elk	*Cervus elaphus*	EQUIVOCAL	Phenotypic plasticity in calving date during a 30 year study	Nussey et al. 2005
Mammalia	Fisher	*Martes pennanti*	EXPANSION	Documented range expansion, related to snow depth	Carr et al. 2007a,b; Voigt et al. 2000
Mammalia	Gray Wolf	*Canis lupus*	EQUIVOCAL	Increased pack size in years with deeper snow	Post et al.1999
Mammalia	Least Weasel	*Mustela nivalis*	EXPANSION	Documented range expansion into Great Plains	Frey 1992
Mammalia	Little Brown Bat	*Myotis lucifugus*	EXPANSION	Energetic limit for hibernation shifting north	Humphries et al. 2002
Mammalia	Lynx	*Lynx canadensis*	CONTRACTION	Lynx-hare cycle related to climate; 175 km contraction of southern range limit in Ontario	Stenseth et al. 1999, Koen et al. 2014
Mammalia	Marten	*Martes americana*	EQUIVOCAL	Possible contraction in response to expanding fishers	Krohn et al. 1995, 1997
Mammalia	Masked Shrew	*Sorex cinereus*	EXPANSION	Increased body size since 1950; documented range expansion into Great Plains	Yom-Tov and Yom-Tov 2005, Frey 1992
Mammalia	Meadow Jumping Mouse	*Zapus hudsonius*	EXPANSION	Documented range expansion into Great Plains	Frey 1992
Mammalia	Meadow Vole	*Microtus pennsylvanicus*	EXPANSION	Documented range expansion into Great Plains	Frey 1992
Mammalia	Mink	*Neovison vison*	EQUIVOCAL	Mink-muskrat cycle related to climate	Haydon et al. 2001
Mammalia	Moose	*Alces alces*	CONTRACTION	Increased disease at southern range boundary; cumulative effects of weather on body condition	Murray et al. 2006, Post and Stenseth 1998
Mammalia	Muskrat	*Ondatra zibethicus*	EQUIVOCAL	Mink-muskrat cycle related to climate	Haydon et al. 2001
Mammalia	Northern Flying Squirrel	*Glaucomys sabrinus*	CONTRACTION	Range contracts in response to competition from expanding southern flying squirrel populations	Bowman et al. 2005, Weigl 1978
Mammalia	Opossum	*Didelphis virginiana*	EXPANSION	Documented range expansion	Kanda 2005, Austad 1988, Myers et al. 2009
Mammalia	Polar Bear*	*Ursus maritimus*	CONTRACTION	Decreasing body condition and productivity, hybridization, population declines	Obbard et al. 2006, Derocher et al. 2004, Stirling et al. 2004, Hunter et al. 2010
Mammalia	Porcupine	*Erethizon dorsatum*	EXPANSION	Porcupines following warming associated poleward shift in tree line; expansion related to reduced winter severity	Voigt et al. 2000, Payette 1987

Mammalia	Raccoon	*Procyon lotor*	EXPANSION	Documented range expansion, related to reduced winter severity	Larivière 2004, Voigt et al. 2000
Mammalia	Red Fox	*Vulpes vulpes*	EXPANSION	Expanding north due to temperatures	Selås and Vik 2007, Hersteinsson and Macdonald 1992
Mammalia	Red Squirrel	*Tamiasciurus hudsonicus*	EXPANSION	Onset of breeding advanced by 18 days over a 10-year study	Réale et al. 2003
Mammalia	Snowshoe Hare	*Lepus americanus*	EQUIVOCAL	Lynx-hare cycle related to climate	Stenseth et al. 1999
Mammalia	Southern Flying Squirrel	*Glaucomys volans*	EXPANSION	Energetic bottleneck shifting north, but dynamic boundary	Bowman et al. 2005, Weigl 1978, Myers et al. 2009,
Mammalia	White-footed mouse	*Peromyscus leucopus*	EXPANSION	Northward range expansion	Myers et al. 2009
Mammalia	White-tailed Deer	*Odocoileus virginianus*	EXPANSION	Cumulative effects of snow depth reduce body condition and fecundity; winter severity causes range contraction	Garroway and Broders 2005,Patterson and Power 2002, Voigt et al. 2000, Post and Stenseth 1999

* Species-at-risk

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